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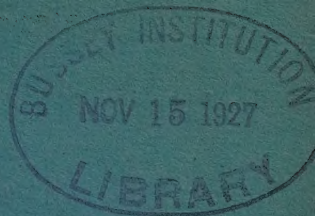
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# ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XI

January, 1927

No. 1

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## AN ECOLOGICAL STUDY OF SOUTHERN WISCONSIN FISHES

The Brook Silversides (*Labidesthes sicculus*) and the Cisco  
(*Leucichthys artedii*) in Their Relations to the Region

WITH 16 PLATES AND 27 TABLES

BY

ALVIN ROBERT CAHN

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Price \$1.50

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PUBLISHED BY THE UNIVERSITY OF ILLINOIS  
UNDER THE AUSPICES OF THE GRADUATE SCHOOL  
URBANA, ILLINOIS



# UNIVERSITY OF ILLINOIS STUDIES PUBLISHED

## ILLINOIS BIOLOGICAL MONOGRAPHS

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# AN ECOLOGICAL STUDY OF SOUTHERN WISCONSIN FISHES

The Brook Silversides (*Labidesthes sicculus*) and the Cisco  
(*Leucichthys artedi*) in Their Relations to the Region

WITH 16 PLATES AND 27 TABLES

BY

ALVIN ROBERT CAHN

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward  
No. 297

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE  
GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1924



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## GENERAL ECOLOGICAL CONSIDERATIONS

## INTRODUCTION

The first section of this paper is intended to serve as a general introduction to a series of ecological studies made upon the fishes of southern Wisconsin. At the present time the writer has a record of ninety species of fishes from within the boundaries of Waukesha county alone, and upon these species a considerable number of ecological studies have been completed. Two of these studies are herewith presented, one on the brook silversides (*Labidesthes sicculus*), the other on the cisco (*Leucichthys artedii*). These have been selected as the first studies presented for three reasons. In the first place, the fishes themselves differ greatly, one being a minnow, the other a valuable game and food fish; secondly, the fishes occupy positions in the lake as widely divergent as possible, the silversides being a surface species, the cisco an inhabitant of the deepest water; and lastly because the study of the cisco brought out a series of ecological problems of approximately ordinary complexity, while the study of the silversides presented a series of problems for solution that is far more complicated than has been encountered in any of the other investigations so far undertaken. The writer feels, therefore, that, taken together, they give a comprehensive idea of the type of problems encountered in a series of ecological studies dealing with the fishes inhabiting our inland lakes.

It is altogether probable that no lakes in the United States have been more carefully or more extensively studied than those of southern Wisconsin, from the point of view of hydrography, morphometry, chemistry and yearly cycle. The pioneer limnological studies of Birge and Juday have yielded a mass of information relating to the behavior and physical and chemical status of these bodies of water which is second to none in the entire country, the closest approach being the "finger lakes" of north-central New York, which is also due largely to the work of these investigators. Their most extensive studies have been made on Lake Mendota, at Madison, Wisconsin, together with Monona and other lakes connected by the Yahara river to the Rock river, but their surveys have encompassed as well the lakes farther east, lying in Waukesha county. As a result of these researches one has very excellent hydrographic and morphometric data invaluable for the further study of aquatic biota of this region. The yearly behavior of the lakes is well known; the progress through the seasons of the thermocline and the associated phenomena have been comprehen-

sively tabulated; the dissolved gases of the water have been extensively studied, and the seasonal variations carefully recorded. Thus, by the foundations laid down by these investigators, the road has been paved for further studies of the lakes of southern Wisconsin, and it must be admitted that, in spite of the excellent beginning that has been made, all the work so far has been only a beginning. Our knowledge of the lakes in question is still only skin deep—surface deep—if indeed it is not merely a ripple on the surface. The work of Birge and Juday has been followed by the studies of Pearse on certain fish occurring in the Madison waters, and by Muttkowski with his quantitative and qualitative study of the fauna of Lake Mendota, with special reference to insect life. Concerning the Waukesha county group of lakes, nothing has been published outside of the work of Birge and Juday, excepting only a few records of fish foods furnished by the writer to Pearse and included in one of his papers (43).

The present paper is, in a way, the result of circumstances. Having lived in Waukesha county for over twenty summers, and having, during the last twelve years, his own private laboratory for carrying on investigations, the present writer has attempted to avail himself of the opportunities lying literally at his door. A serious study of the fishes of the region was begun in 1914 when, as a graduate student at the University of Wisconsin, the writer undertook an intensive study of the life history of the cisco (*Leucichthys artedi* (LeSueur)) in Lake Mendota and in the Waukesha county lakes which contain the species. A collection of the various species of fishes of the region was begun long before this date in an effort to ascertain what fishes inhabited the lakes and rivers. While the original idea encompassed only a listing of the species, this was enlarged in 1915 to include an intensive study of every species possible. Thus the study of the biology of the cisco was subordinated to a study of the biology of the fishes of the region, and forms one of a series of studies dealing with ecological life history investigations of individual species.

This series of papers, of which this is the first, purports to be a series of ecological studies made upon the fishes found within the boundaries of Waukesha county, Wisconsin, together with certain observations made upon identical species in other regions of the state where opportunities or facilities proved more advantageous for carrying on the work. The data presented are entirely original unless otherwise specifically stated. These include the results of something over one hundred gas analyses to determine the position of the thermocline in various lakes at different times of the year in order to ascertain its effect upon the distribution of the fishes; over two thousand H-ion determinations, accompanied in some cases by oxygen determinations, in an effort to discover if either of these factors is responsible for certain behavior phenomena; thousands of temperature readings at all depths of water, and many visibility readings by means of

Secchi's disc. The fish have been collected from practically every lake, and from all rivers and streams. In collecting fish, gill nets were used. For the smaller species and the young of the larger, minnow nets of various lengths were drawn where opportunity afforded. When physical conditions rendered this method impossible and in all streams where a current made it practicable, the glass minnow trap was used with excellent results. It is impossible to state exactly how many collections were made as in the early stages of the investigation the only records kept concerned the presence or absence of species; however, beginning with 1918 the following number of collections are recorded: 1918—216; 1919—none, due to the presence of the writer in France; 1920—547; 1921—520; 1922—738; 1923—1,264; a total of 3,285. Certainly well over 4,000 are represented. Further information has been obtained by examining the catches of commercial fishermen who nearly every fall seine in the neighborhood. By this means many data have been accumulated regarding the relative abundance of species, together with information dealing with size and growth otherwise unobtainable. The investigations have been, perforce, largely carried on during the summer months, but from two to three weeks have been spent in the region every winter, during which time the condition of the lakes and the fish in winter have been investigated. All identifications have been made by the writer and in every case this has been checked by an expert ichthyologist.

In presenting this paper the writer wishes to express his appreciation to several gentlemen whose kindly encouragement and ever-ready advice have made the pursuance of the problem a real pleasure: to Dr. A. S. Pearse, under whose guidance the problem was originally begun; to Dr. Bashford Dean and to Dr. T. L. Hankinson, who have checked up identifications of the fishes involved; to Dr. H. B. Ward whose suggestions and criticisms have always been freely given, and to Dr. V. E. Shelford, at whose suggestion several hitherto uninvestigated angles of the problem were undertaken and under whose guidance the innumerable loose ends accumulated during something like twelve years of investigation were drawn together and synthesized. To these the writer finds it a rare privilege to express his sincere thanks.

#### REGION UNDER DISCUSSION

Waukesha county, Wisconsin, with an area of 560 square miles (Fig. 8), lies in the second tier of southern counties of the state, with its eastern boundary about twenty miles west of Lake Michigan, Milwaukee county intervening. Of this area, the northwestern quarter, comprising some 170 square miles, is the center of the investigations considered in this report, and is the so-called "Oconomowoc-Waukesha lake district." This region extends from the Ashippun river on the north 14 miles south to Hunter's



lake, and from Golden lake on the west 12 miles east to Pewaukee lake and the Fox river. Within the rough rectangle thus formed lie no fewer than forty-five lakes of various sizes, ranging from Pewaukee lake with an area of 2,297.8 acres down to such small bodies of water as Washtub and Mud lakes, with an area of three or four acres only. Of these, twenty-five of the largest and most important have been surveyed, and their depth, area, shore-line and general topography recorded by Birge and Juday (1914). These lakes show a total water surface area of 9,971 acres. Besides these lakes five river systems drain the region, and there are many streams of lesser magnitude.

Outside the Oconomowoc-Waukesha group the county contains a number of lakes of considerable size, scattered over the remaining three-quarters of the area. The largest of these, Muskego, near the town of that name in the southeast corner of the county, nearly equals Pewaukee in size, but it has never been surveyed, and its exact area is unknown. Here, too, lie Little Muskego, Denoon, Muckwonago, Phantom, Eagle, and many smaller unsurveyed lakes, all of which, however, are included in this report. In the northeast corner of the county there are no lakes, but here is found the Menomonee river, which introduces the Lake Michigan drainage area into the scope of the investigation, along with which come several species of fish found in no other part of the county. The lakes and river systems will be listed subsequently.

The region under discussion is of importance in connection with the work of Dr. Stephen A. Forbes and R. E. Richardson, together with their associates in the Illinois State Natural History Survey, because within it lies the source of the Fox river of Illinois, together with a great number of lakes and several river systems which flow into the Rock River and the Illinois, on which rivers the Illinois Natural History Survey is working so intensively. The region is, therefore, one of the great tributary areas to the river systems upon which they are focusing their energies.

The lakes of Waukesha county owe their origin to the action of the great ice sheet which featured the pleistocene epoch of the quaternary period. There were several great movements north and south of the Labrador glacier and other huge ice masses hundreds of feet thick. These glaciers crawled southward from their northern source, then slowly retreated, causing great changes both in the topographic and climatic conditions of the regions invested, and it is largely to the influence of this glacial movement that is due the present day distribution of the plants and animals both within the territory concerned and the adjacent regions. There seem to have been at least three—probably five—more or less distinct advances of the ice, the three most important being the Pre-Wisconsin, the Early Wisconsin and the Late Wisconsin, and it is to the last of these invasions that is traced the origin of the Waukesha county lakes.

At this time the invasion came from the Labrador glaciers and the movement was in a southerly direction, with a slight westerly trend. The movement of the ice sheet followed in a general way the already formed basins of the Great Lakes, and overflowed into the surrounding country (Fig. 9). As a result of this guiding of the course of the glacier, the ice mass assumed a lobate form, coinciding roughly with the general shore line of the basin down which it flowed. Thus the glacier that came down the basin of Lake Michigan, known as the Michigan glacier, put out a lobe, or sub-glacier, which traveled down the basin formed by Green Bay, and is known as the Green Bay glacier, while the ice mass occupying the basin of Lake Superior sent out smaller lobes which followed roughly the larger bays of its shore line. Following the outline of the glacier westward, one finds a series of smaller lobes and glaciers, the Langlade, Wisconsin Valley, Chippewa and Superior off-shoots which, however, did not reach far into the state, and which are of no significance in so far as the present paper is concerned.

By referring to figure 9 it will be seen at once that the edges of the Michigan glacier and the Green Bay glacier came in contact for quite a distance. As a result of this contact, and because each glacier was acting as an independent unit, the adjacent lateral moraines also came together and were built up side by side as a continuous ridge, forming a *medial* moraine which, because of its very broken and uneven appearance, is of the type known as a *kettle* moraine, extending as a ridge of glacial deposit down the middle of the apparently united ice mass. In this manner was formed the ridge of broken hills, over one hundred and fifty miles in length, which crosses Waukesha county in a northeast-southwest direction, forming the most important topographic feature of the landscape. Within the county the highest point in this ridge is Government Hill, with an elevation of 1,233 feet. With the retreat of the glacier, not only was this great moraine left stranded, but great blocks of ice were broken off and remained imbedded in this moraine area. These melted with the advance of the warmer climate accompanying the retreat of the main body of the ice, and left innumerable depressions varying in size from "pot-holes" a few yards in diameter to lake basins having an area of over a thousand acres. Some of these depressions filled with water, the source of which was surface drainage and a multitude of springs, and formed the abundant lakes of the district. In this manner all the lakes of the county were formed, with the exception of Pewaukee lake, which lies outside the area of the kettle moraine. This lake differs, then, from the others in that it lies in the area of the ground moraine, and occupies a shallow valley which resulted from the failure of the glacier to fill in this basin with ground moraine deposits. At the same time that the lake basins were being laid out, the general plan of the river systems were being formed, with the natural result



that the river beds form a series of connecting channels between the various lakes.

After the formation of the lakes, it was a simple matter, as has been said, to establish connections between the lakes by means of river systems. The second source of water in the lakes is springs, which are extremely abundant throughout the region. Practically all of the lakes, whether they have inlet and outlet or not, are spring fed. These springs are the termini of great under ground water systems, and arise in the bottom of the lakes as bubbling streams. Nothing is known at the present time concerning the abundance of these springs in any lake, but data at hand indicate that they are numerous. In many places along the shores these springs have been "captured" and show an output of a vast quantity of marvelously clear, cold water, which is none other than the famous "Waukesha water" for which the county is well known. The temperature at which these springs enter the lakes is very low, the temperature of nine springs, taken in June, being as follows: 5.1, 5.4, 5.0, 4.8, 5.8, 5.6, 5.0, 4.9, and 5.0 degrees centigrade.

The medial moraine, to which I have previously referred, divides the county into two primary drainage areas, namely that of 1) the Rock river and 2) the Fox river. The northwestern third of the county contributes either directly or indirectly to the Rock river, while the southeastern third contributes to the Fox river drainage basin. Both of these rivers are tributaries to the Mississippi within the boundaries of Illinois, the Rock river entering directly, the Fox river by its union with the Illinois river. The northeastern third of the county lies outside of the Mississippi drainage, its one river, the Menomonee, flowing almost due east into Lake Michigan.

There are five river systems within the county, and these may be tabulated as follows:

1. Rock river tributaries:
  1. Ashippun river.
  2. Oconomowoc river.
  3. Bark river.
    - a) Scuppernong river and creek.
2. Illinois river tributaries:
  4. Fox river.
    - a) Muckwonago river.
    - b) Pewaukee river.
3. Lake Michigan tributaries:
  5. Menomonee river.

An examination of the map will show that a vast majority of the larger lakes are arranged in two chains, the component lakes being connected

by rivers. These chains lie in a general northeast-southwest direction, and are the courses of the Oconomowoc and Bark rivers. Of the five river systems listed, it is of interest and importance to note that of the twenty-eight most important lakes of the county, no less than eighteen fall into these two chains, a condition which permits the passage back and forth of at least the smaller species of fishes, and of the fry of the larger species. The relation existing between the lakes and the river systems is indicated herewith:

1. Oconomowoc river system:

- |                   |                     |
|-------------------|---------------------|
| 1. Lake Keesus.   | 6. Garvin Lake.     |
| 2. North Lake.    | 7. Oconomowoc Lake. |
| 3. Pine Lake.     | 8. Fowler Lake.     |
| 4. Beaver Lake.   | 9. Lac La Belle.    |
| 5. Okauchee Lake. |                     |

2. Bark river system:

- |                          |  |
|--------------------------|--|
| 10. Nagawicka Lake.      | 15. Crooked Lake.                                  |
| 11. Upper Nashotah Lake. | 16. Golden Lake.                                   |
| 12. Lower Nashotah Lake. | 17. Hunter's Lake (Scuppernong creek and river).   |
| 13. Upper Nemahbin Lake. |  |
| 14. Lower Nemahbin Lake. | 18. Dutchman's Lake (Scuppernong creek and river). |

3. Fox river system:

19. Pewaukee Lake.
20. Muckwonago Lake.
21. Phantom Lake (Muckwonago river).
22. Eagle Lake (Muckwonago river).
23. Lulu Lake (Muckwonago river).
24. Millpond Lake (Muckwonago river).

4. Ashippun river system:

25. Ashippun Lake.

The Menomonee river receives the water from no lake within the limits of the county, while there are nine lakes of some importance that have neither inlet nor outlet:

- |                  |                        |
|------------------|------------------------|
| 1. Genesee Lake. | 6. Henrietta Lake.     |
| 2. Otis Lake.    | 7. Silver Lake.        |
| 3. Duck Lake.    | 8. Pretty Lake.        |
| 4. Mouse Lake.   | 9. Little Silver Lake. |
| 5. Forest Lake.  |                        |

The Ashippun river, a small stream which rises to the northward in Dodge county, enters Waukesha county from the north, then bending sharply westward, drains a narrow valley in the northwest corner of the county. It is a slow, shallow stream which flows for the most part between



low, swampy banks in a bed that is made up largely of soft muck. It varies in width from twelve to nearly fifty feet during the early summer, but the end of the warm weather often finds the stream reduced nearly to a minimum. A number of gravel areas occur and here riffles afford local swift water habitats, characterized by typical swift water species of fishes. Plant growth is abundant and during the late summer the stream becomes practically choked with thick beds of *Potamogeton*, *Nymphaea* and limnophilous species of filamentous algae, while areas of *Ceratophyllum* occur particularly in regions of entering springs. The stream has a total length within the county of approximately sixteen miles, and has no tributary streams of consequence. It enters Rock river three quarters of a mile west of the county line, the closest approach of Rock river to Waukesha county.

The Oconomowoc river drains a long, torturous, but rather narrow valley lying south and east of the Ashippun drainage. Serving, as it does, as a connection between a large number of lakes, and as it is a river of considerable size, it affords an important fishway. Innumerable streams and creeks, all of them spring fed, are tributary to it in the northern portion of its course, of which the Little Oconomowoc and Mason creek are the largest. In its northern reaches the river flows through a low, swampy, spring-fed country of loose black muck, varied with areas of gravel and sand. For the most part it is slow and sluggish, but there are occasional regions of considerable drop, where swift water habitats predominate. Such areas are plantless, while in the sluggish regions *Potamogeton* sp., *Elodea canadensis*, *Nymphaea advena*, *Chara* sp., and *Vallisneria spiralis* occur in considerable abundance, but not thick enough to choke the river. In stagnant backwaters local regions of *Lemna minor* are found. Important as is the river as a fishway, its value is greatly reduced by the presence of six dams—Monches, North Lake, Okauchee Lake, Oconomowoc Lake, Fowler Lake, and the outlet of Lac La Belle. These dams afford a downstream passage for many species of fish, but are impassible barriers in upstream migrations—particularly the spring and fall migrations of the pickerel (*Esox lucius*), suckers of various species, and cisco (*Leucichthys artedii*). As the river flows into Rock river six miles west of Lac La Belle, the river is a constant source of supply of valuable game fish to the Rock river, while this river can contribute nothing at all to the Oconomowoc river above the outlet of Lac La Belle. It must therefore be considered as an important fish tributary to the Rock river.

The Bark river cuts a diagonal from the northeast to the southwest just northwest of the center of the county, draining a large area lying north of the main ridge of the kettle moraine. Its course is through a rich farming country, and it is not until it approaches the western limits of the county that it encounters large swamp areas. This is due to the fact that the greater

part of its course parallels the base of the moraine, but tends to leave it near the western limit of the county. For the most part it has cut a bed through rich black soil, flowing in a channel from ten to thirty feet wide. Its bed is characterized by many deep pockets located with definite relation to the innumerable bends in the course of the river, these holes affording ideal places for game fish. Areas of swift water occur, in which a fine gravel bottom affords habitat for swift water forms and offers breeding grounds in abundance for the many species of minnows choosing such localities. As a fishway it is far more important than the Oconomowoc river because of the lack of dams. A dam at Rome a short distance west of the county line has flooded a large area which abounds in game fish, and there is no serious barrier to river migration in both directions nearly across the entire county (to Merton). This is especially important because of the number of lakes involved in the course of the river. One important tributary the Bark river has in Scuppernong creek, which edges in between Bark river and the moraine as the former leaves the higher ground. This stream drains a large area of swamp land, and exchanges with the Bark river an abundant fish population. Still farther to the south the Scuppernong river intrudes between the Bark river and the moraine. This river rises in Little Silver lake, a small, spring-fed body of water, and flows through a vast swamp area in the southwest corner of the county, to unite with Bark river south of the town of Hebron in Jefferson county. Within the county limits it is a small river of very soft bottom and water stained a deep brown from the decomposition of organic matter.

The Fox river rises from a series of springs in the northeastern corner of the county, a short distance north of Lannon. From here it flows in a general southwesterly direction, its valley lying between two morainic ridges. Its course takes it through regions of rock and swamp, agricultural land of high quality and regions of gravel, so that the bed of the river offers an alternation of conditions which meet the requirements of a wide range of species of fishes. Near its source it is a tiny stream with patches of Potamogeton furnishing shelter for many head-water species of minnows as well as to the grass pickerel (*Esox vermiculatus*), this representing one of the most northern records of the species. Within eight miles of its origin the river widens rapidly and becomes a stream over a hundred feet wide as it flows through the city of Waukesha. From here it traverses vast swamp areas where it receives many small tributary creeks. It abounds in carp (*Cyprinus carpio*) whose great numbers and constant activity keep the water in a constantly muddy condition. At this point its general course is almost due south, and it leaves the county as a river more than two hundred feet wide with low, boggy, undercut banks and water of a deep brown, opaque appearance. Throughout its entire course within the county its flow is unobstructed, affording excellent opportunities for fish



movements in both directions. Its chief tributary is the Pewaukee river, the outlet of Pewaukee lake.

The Menomonee river rises in Washington county just north of the northeastern corner of Waukesha county, through which it flows in a northeasterly direction. It is a very small stream, flowing almost entirely through limestone (Niagara) formation. Its bed is a mass of limestone rocks which afford no footing for plant growth, so that both plants and fishes are few. Occasional areas of swamplands bound the river as it progresses eastward, and here there is an abundance of minnow life very different in composition from the other river systems, none of which are tributary to Lake Michigan into which the Menomonee empties via a short connection with the Milwaukee river within the city limits of Milwaukee. Within Waukesha county it has but one tributary stream, the Little Menomonee, which joins it from the north. Within the county there is no place at which the river is large enough to offer game fish habitation, but it is of importance to the fish fauna of the county, introducing as it does a number of species not found in the western part of the state—the Rock river and the Illinois river tributaries.

As has already been mentioned, the vast majority of the lakes of the county fall into a series of chains with river connections. There remain, however, a great number of small lakes, almost too many to count, unless one designates a minimum size as to what constitutes a "lake"—which lie outside of these river systems, and which have neither inlet nor outlet. The larger of these I have already listed. However, many small lakes abound. North of Okauchee lake lies a series of lakes, some seventeen in number, all containing fish life, which are known as the Skidmore ponds, and similar areas are found scattered over the county. All of these are relatively small in size and all occupy depressions in morainic areas. Most of them are quite deep—much deeper than their size would lead one to infer—and all are spring fed, relying upon springs and surface drainage and rainfall as their source of water supply. Many of these lakes lie in swamp areas, and are the last remnants of former lakes of considerable size, though of little depth. In many cases the former shoreline of these old bodies of water is plainly visible, being indicated by gravel terraces.

Although all of the lakes are of practically the same age, the smaller ones in many cases already show marked indications of old age. The encroachment of the shore vegetation upon the lake is very evident, as shown in the photograph of Laura Lake, while the old lake bed and an island which is now a point is clearly shown in Plate I. The larger lakes, naturally, show less evidence of ageing, though of course the process is going steadily on.

The water of all of the larger lakes is remarkable for its purity and clearness, and none of the lakes within the county suffer from the pollution

so common to the lakes and streams of Illinois. The clearest of all the lakes is Upper Nashotah, with Oconomowoc second and Lower Nashotah third. By use of the Secchi disc, a white enamel disc 10 cms. in diameter, the visibility of these lakes has been tested, with the following results:

	June	February
Nashotah, Upper	605 cms.	728 cms.
Oconomowoc	587 "	697 "
Nashotah, Lower	524 "	632 "
Lac La Belle	354 "	572 "
Fowler	368 "	570 "
Nemahbin, Upper	365 "	368 "
Nemahbin, Lower	330 "	345 "
Pine	345 "	340 "
North	351 "	334 "
Pewaukee	258 "	316 "
Dutchman's	195 "	287 "
Silver	208 "	281 "
Laura	84 "	103 "

The shoreline of all of the lakes is constantly undergoing change and, although this alteration is almost imperceptible from year to year, yet it has an important effect upon the lakes. This action is two-fold: 1) that of the waves, and 2) that of the ice. The constant attack of the water upon the shores is constantly eating away the shoreline and the material thus removed is carried out to be deposited eventually in the lake. This action has in the course of time profoundly changed the shoreline of the lakes, and has built up a characteristic series of sand bars which extend around the lakes at a varying distance from the shore. This is particularly true in the case of all lakes lying in a sand-gravel formation and less true in the case of those small lakes lying in a loose, black muck soil. This muck tends to a far more uniform deposition and consequently is deposited more nearly over the entire lake bottom, and bars do not occur. Such facts are of extreme importance to the fish life of the lakes as the presence or absence of bars may in many cases mean the presence or absence of breeding grounds, which in turn limits the possible species population.

As has been stated, most of the larger lakes of the county have been surveyed by the Wisconsin Geological and Natural History Survey, and their hydrography and morphometry is well known. The results have been published by Birge and Juday (1914) and the reader is referred to this work if details are desired. The following table has been compiled from that source in order to bring the general facts into this paper for ready reference.

TABLE 1  
DATA ON THE LAKES OF THE OCONOMOWOC-WAUKESHA GROUP  
(Compiled from Birge & Judav)

Lake	Area in Acres	Max. Depth: Meters	Ave. Depth: Meters	Shore- line: Km	Volume: Cubic Meters.
La Belle	1,137.4	14.2	3.3	12.5	15,165,000
Fowler	83.5	15.2	4.4	1.5	1,478,500
Oconomowoc	631.3	19.1	9.5	7.5	24,303,000
Oconomowoc, Bay	170.8	15.0	7.9	3.7	5,750,000
Okauchee	1,056.7	28.6	12.1	17.9	43,721,000
Mouse	90.4	20.2	9.1	3.9	3,092,000
North, East	329.0	23.7	12.7	5.2	17,020,000
North, West	115.3	22.4	11.4	2.7	5,329,000
Pine	755.5	27.4	12.1	10.9	37,015,000
Beaver	305.5	15.0	5.1	5.4	6,312,000
Nagawicka	917.6	28.8	11.0	11.3	40,961,000
Pewaukee	2,297.8	13.8	3.9	19.5	36,694,000
Nashotah, Upper	136.8	15.6	7.0	3.5	3,885,000
Nashotah, Lower	100.5	14.1	6.1	3.0	2,498,000
Memahbin, Upper	270.9	18.9	9.0	4.5	9,958,000
Nemahbin, Lower	265.5	10.8	2.5	4.1	2,670,000
Crooked	54.8	4.8	1.9	2.9	425,000
Genesee, South	62.7	14.5	6.7	1.9	1,717,000
Genesee, North	102.0	11.1	4.5	2.4	1,865,000
Silver	231.9	13.4	4.8	4.6	4,499,000
Garvin	21.7	11.0	5.0	1.3	435,800
Otis	40.0	8.6	4.9	1.9	789,000
Eagle	211.2	1.5	...	...	...
Keesus	236.8	12.5	...	...	...
Golden	256.0	13.0	...	...	...
Denoon	185.6	19.0	...	...	...
Five	128.0	5.0	...	...	...
Muskego, Big	2,739.0	8.0	...	...	...
Muskego, Little	518.4	14.0	...	...	...
Phantom	108.8	8.5	...	...	...

## CLIMATOLOGY

Waukesha county lies within the zone of influence of Lake Michigan, which tends to temper the summer heat. Winds off the lake lower the temperature and tend to increase the relative humidity. Winters are ordinarily severe, with the temperature dropping as low as  $-28$  (Jan. 17, 1924). Precipitation (Fig. 10) is abundant and affords an enormous supply of water directly to the streams and indirectly to the lakes. This causes a seasonal fluctuation in the water level of the lakes, which has a certain influence upon some species of fish. It is of particular importance to the pickerel (*Esox lucius*) as the excessive amount of water inundates the swamps bordering the lakes, affording excellent weedy breeding grounds



for the species, but the drop in level occurs often before the eggs mature and a majority of them are left stranded and never hatch. During the winter the formation of the ice plays an important part in the life of the fish of some lakes—as Mud lake north of Pine lake—where, if the ice forms in excessive thickness and so completely as to leave no free water, thousands of fish of all species are killed from a lack of oxygen. Such lakes are deficient in springs, and with the cutting off of the contact between the water and air, oxygen deficiency occurs. Such a condition a number of years ago completely robbed Washtub lake of its entire larger fish fauna—sunfish, perch, bass, pickerel, carp—leaving it almost a dead lake. Winter fishing through the ice is of great importance as thousands of perch, silver bass, pickerel, cisco, white bass and wall-eyed pike are caught at a time when the species (excepting only the cisco) are heavy with spawn. The result is a serious drain on the fish population, which is offset only to a slight degree by the food value of the fish—most of the fish caught are sold in spite of the law—with the maximum amount of waste and the minimum amount of sport.

TABLE 2  
CLIMATOLOGICAL DATA FOR WAUKESHA COUNTY, WISCONSIN  
(City of Waukesha; elev. 864 ft.)

	1913	1914	1915	1916	1917	1918	1919	1920	1921
Maximum Temperature.....	97	95	87	103	98	102	101	93	100
Minimum Temperature.....	-12	-20	-23	-17	-18	-23	-21	-15	-3
Average Temperature.....	47.2	43.8	43.6	45.7	42.7	46.5	46.3	45.9	50.2
Maximum Monthly Precipitation.....	7.06	6.90	10.0	6.60	7.44	5.60	6.97	4.71	9.50
Month of Maximum Precipitation.....	9	9	6	6	9	5	5	3	9
Minimum Monthly Precipitation.....	.49	?	.65	.41	.38	1.29	.32	.38	.30
Month of Minimum Precipitation.....	12	?	12	7	11	9	1	2	1
Total Precipitation.....	39.7	32.7	32.68	42.3	35.0	30.4	36.9	30.5	40.4
Total Snowfall.....	39.4	47.1	?	58.0	35.9	71.0	43.7	35.0	31.9

Mean annual temperature for 25 years.....46.0

Mean annual precipitation for 28 years.....30.16 inches.

#### LAKE CONDITIONS

One of the most significant features of the lake environment is the seasonal cycle which the waters undergo. These changes are both thermal

and chemical, and are the direct results of atmospheric, or at least non-aquatic conditions. The prime cause of these changes is the warming of the water due to the activity of the sun's rays during the spring and summer, and the subsequent cooling again as the sun drops to the north. During the winter, when the lake is covered with ice, the aquatic environment is in a state approaching stable equilibrium and a constant temperature, equal oxygen and carbon dioxide distribution is found from top to bottom. Under these conditions there is a complete circulation of the water and, because of the uniform distribution of the gases, the entire lake is accessible—at least insofar as the gas content of the water is concerned—to fish life. This is particularly important for the deep water species as *Leuciscus artedi*, for example, as will be discussed in the section dealing with the cisco. Thus the lake starts out in the early spring with a uniform temperature normally below 4°C, and a uniform gas distribution. With the warming of the surface water, the complete circulation of the water is checked and the lake becomes divided into two regions, separated from each other by a sharp break in temperature. This break is the thermocline, the warmer region above it is known as the epilimnion, the cooler region below it as the hypolimnion. The position of the thermocline is at first in deep water, but with the continued warming of the water the thermocline crawls slowly upward until in mid-summer the hypolimnion greatly exceeds the epilimnion in depth. These temperature changes which check the free circulation of the water result in marked changes in the gas content of the water, as the oxygen content cannot be restored, nor the carbon dioxide distributed. The result is that the hypolimnion becomes an area deplete in oxygen and replete in carbon dioxide, forming a region into which fish may venture only for a short period of time. Thus, through the formation of the thermocline, a large portion of the lake becomes unsuited for fish life, and a consequent movement of the deep water fish to shallower waters results. This seasonal cycle has been well worked out for many Wisconsin lakes by Birge and Juday, including many of the Waukesha county lakes.

The importance of these seasonal changes in oxygen, carbon dioxide content and temperature variations of the water will be fully discussed in their relation to the distribution of fish life in the section dealing with the life history of the cisco (*Leuciscus artedi*). Suffice it here to say that the behavior of the thermocline offers barrier conditions which force the deep water species of fish to leave the deep places and seek more favorable conditions of gas content of the water. The serious results which accrue when the thermocline forces these deep, cold water species up into the zone of warm surface water to which they are not tolerant, will also be discussed in that section.

Still another problem that assumes an important rôle in the life history of various fish is the hydrogen ion concentration of the water. Insofar as the lakes are concerned, the range of variation is not great within the county, all of the lakes investigated being alkaline from the surface to the bottom. This is in spite of the acid condition of much of the spring water which forms one of the main sources of water supply to the lakes. Throughout the summer of 1923 a total of 634 hydrogen ion concentration determinations were made by the colorimetric method in the various lakes, at different depths, day and night. During the first ten days of February, 1924, a series of 160 readings was made to determine the winter conditions in respect to the ionic concentration. In collecting the samples of water for the determinations, a special apparatus designed by Shelford (1923) was used, consisting of a specially designed pump with two-way pet cocks, by means of which a vacuum is established within a small test tube and a sample of water drawn in without contact with air. Into this tube the two drops of indicator were injected through a rubber membrane by means of a hypodermic outfit, and the concentration read and compared with the standard series of tubes. A long rubber hose with a hole diameter of 1 mm. was used in bringing up the sample, and for bottom work a pan designed for the purpose of confining a local area of water assured the sample being of the region desired.

The results of the field work show that there is a definite relation between oxygen content of the water and the H-ion concentration, which may be stated: 1) As the oxygen content of the water *decreases*, the H-ion concentration *increases*. 2) While ordinarily there is an increase in CO<sub>2</sub> accompanying a decrease in O, the H-ion concentration seems to bear very little if any relation to the CO<sub>2</sub> changes: that is, changes in O are regularly accompanied by changes in the H-ion concentration in the opposite direction, while changes in the CO<sub>2</sub> content either may or may not be accompanied by a change in the H-ion concentration.

The following table, 3, gives a partial summary of a part of the data:

TABLE 3  
Showing Gas and Temperature Conditions at Different Levels in  
Characteristic Wisconsin Lakes

Date	Lake	Depth in meter	pH	O	CO <sub>2</sub>	Temp.
June 12, 1923	Oconomowoc	0	8.3	10.1	-3.0	22.1
		5	7.7	10.8	-2.2	18.2
		10	7.6	8.6	1.5	13.8
		15	7.3	5.6	1.7	9.6
		20	7.3	5.1	1.7	5.6



June 29, 1923	Oconomowoc	0	8.2	10.3	-3.1	23.0
		5	7.8	10.1	-1.9	19.3
		10	7.3	5.6	-1.2	14.7
		15	7.2	5.5	1.8	9.2
		20	7.2	5.2	1.6	5.4
July 1, 1923	Lac la Belle	0	7.9	6.2	0.8	27.3
		5	7.8	6.6	-0.2	25.7
		10	7.8	5.9	0.6	13.6
		15	7.3	4.4	1.2	9.4
July 25, 1923	Oconomowoc	0	8.2	8.1	-4.3	28.6
		5	7.5	6.8	-4.2	23.1
		10	7.5	5.6	-1.2	15.2
		15	7.2	1.7	1.1	8.0
		20	7.2	1.1	1.0	6.9
August 24, 1923	Oconomowoc	0	8.2	7.6	-6.2	30.4
		5	8.0	6.8	-4.1	26.8
		10	7.4	1.0	1.0	13.7
		15	7.2	0.7	1.7	9.1
		20	7.1	0.1	2.1	7.4
February 3, 1924	Oconomowoc	0	7.8	7.4	1.9	2.9
		5	7.6	7.4	1.9	3.5
		10	7.6	7.4	1.9	3.5
		15	7.6	7.4	1.9	3.6
		20	7.5	7.4	1.7	3.6

The work of Shelford (1923), Powers (1921), Wells (1915), and others has indicated that the H-ion concentration plays an important rôle in the distribution and behavior of fishes. That this is true has been demonstrated by the writer both in the laboratory and in the field, and will be discussed in considerable detail in the subsequent sections of this paper, and in later papers dealing with the life histories of the different fishes.

#### ECOLOGICAL HABITATS OF FISHES

It is well to glance for a moment at the various aquatic habitats existing within the area. For this purpose one can divide the fresh water environments as follows:

##### I. Rivers and streams.

1. Rapids or rock-bottoms.
2. Sand or gravel-bottoms.
3. Silt, or sluggish-streams.
  - a. Bare bottom.
  - b. Vegetation.

##### II. Lakes.

1. Open water.
2. Eroding rocky-shores.
3. Depositing sandy-shores.
4. Vegetation.
  - a. Submerged vegetation.
  - b. Emerging vegetation.

**Rapids or rock-bottoms:** In this group one finds those species which are found commonly associated with swiftly flowing water which, in the region under discussion, is normally over a rock bottom. These fish have a common ability to maintain themselves in the swiftly flowing water, and agree in an ecological sense in at least two factors: 1) a thigmotactic reaction to large objects; and 2) a positive rheotaxis. Among the most typical fishes are the darters, the miller's thumb, the stonecat and the hog-nosed sucker.

**Sand or gravel-bottoms:** Normally a habitat of less swiftly flowing water and a bottom of finer material than the preceding. This is the habitat which comprises most of the rapid water streams of the region. It is for the most part without heavy vegetation, though islands of Potamogeton and other aquatic plants intrude and afford regions of very temporary shelter to the fish of the open waters. Here one finds the chubs, shiners, various species of darters and stone rollers as typical species.

**Silt or sluggish-waters:** These are the waters found commonly in regions where the streams traverse swampy lowlands. The banks are usually steep, the bottom offering very uncertain footing to one who would seine. The current is slow and sluggish, the water often a dark color both because of the organic matter in solution and because of the black silty nature of the stream bed. The non-vegetated areas are in this condition because of the lack of solid bottom for the insertion of the roots of aquatic plants, and the shifting nature of the bottom material. Such habitats ordinarily have fairly deep water, and are inhabited by carp, suckers, pickerel and a few darters. The vegetated associations are of a similar structure but with a bottom hard enough to afford footing for Potamogetons, Elodea and various other aquatic plants, including masses of filamentous green algae.

**Open waters:** The deep water habitats of the lake, and including everything from the surface over deep water to the bottom. These are the least populated habitats of the lake; the fish are mostly suckers and ciscos on the bottom, and silversides and gar on the surface, with a large zone between which is for the most part uninhabited by fishes or at best receives but a transient population. The lower regions of this habitat are rendered uninhabitable during the summer by the formation of the thermocline.

**Eroding rock-shores:** For the most part shallow water habitats, which are characterized by the eroding action of the waves. These are rough of bottom, and afford certain ecological affinities with the rocky-bottom communities of the streams and rivers. Vegetation is practically lacking, due to the character of the bottom and the action of the waves. It is the home of various darters, minnows of many species and the young of several species of the Centrarchidae.

Depositing sandy-shores: Another habitat scanty in vegetation, this time because of the constant deposition of sand and shore material by the water. The bottom is much less rugged, and shows affinities to the sand and gravel-bottom stream communities. (Fig. 4.)

Vegetation covered areas: These are characteristically of two kinds: 1) the submerged vegetation of the mediumly deep water; and 2) the emerging vegetation, characteristically in shallow water. The submerged vegetation reaches its maximum depth at the edge of the sand bars in water of from fifteen to thirty-five feet in depth, depending on the specific character of the lake. Here great beds of *Potamogeton*, *Nymphaea* and *Vallisneria* afford the normal habitat of the basses, pickerel, dogfish, adult sunfishes, silverbasses and other species. The zone of emerging vegetation, largely rushes, arrow-head and lilies, offers protection to hosts of minnows and the young of many of the larger game fishes.



FISHES OF SOUTHERN WISCONSIN (WAUKESHA COUNTY)  
Order RHOMBOGANOIDEA

Family LEPISOSTEIDAE

1. *Lepisosteus osseus* (Linn.). Long-nosed Gar; Billfish.

Common in all of the larger lakes in the Oconomowoc and Bark river systems, as well as in Pewaukee and Ashippun lakes. During the greater part of the year the gar is a characteristic species of the topmost stratum of the pelagic environment. A gregarious species, it spends most of its time just under the surface, most commonly over deep water. In the spring and during the breeding season (May and early June) the fish often ascend the rivers to spawn, or deposit the eggs over the weed beds of the shallower waters. The young hatch in from six to eight days, depending upon the temperature of the water, and show a marked tendency to come inshore shortly thereafter. During late June young gar two inches or less in length are often taken from weeds by means of minnow seines drawn along the lake shores. Their growth is very rapid, the young fish attaining a length of five to six inches by the end of the first summer. As they grow, they tend to leave the shore environment and assume their position over the deeper water. The food of the adult is almost exclusively minnows, such as *Labidesthes sicculus*, *Fundulus notatus*, *Notropis blennius*, but the young of game fish are sometimes found in stomach examinations. Thus I have taken *Micropterus salmoides*, *M. dolomieu*, *Leucichthys artedi* and *Roccus chrysops* on numerous occasions. The food of the very young consists almost entirely of entomostraca of a variety of species, but very small minnows appear early in the diet of the fish. About 50% of the food of a gar two and a half inches long is fish life. Minnows are always captured sidewise, after which the gar is likely to descend to a considerable depth while the prey is juggled about and worked into position to be swallowed head first. Economically, the species is of little importance; they are of no food value and do considerable damage by the destruction of the young of food fishes.

The short-nosed gar, *Lepisosteus platostomus* Raf., has not been taken by me within the county, but there are records of the species from Rock river near the mouth of the Oconomowoc river, only a short distance from the Waukesha county line.

Order CYCLOGANOIDEA

Family AMIIDAE

2. *Amiatus calvus* (Linn.). Dogfish; Bowfin.

A very common species in practically every lake of any size in the county. An inhabitant of weed beds, the dogfish is found most commonly just over the edge of the bars where heavy beds of *Potamogeton* offer a congenial environment. Breeding begins early, probably often late in April but more frequently early in May, the nesting site preferred being weed beds in water from three to five feet in depth. As I have seen many nests guarded by the parent fish, I conclude with Reighard that it is always the male that protects the nest and guards the young after they leave the nest. The eggs hatch in from nine to twelve days, depending upon the water temperature, and the young fish remain for a little over a week within the confines of the nest. Thereafter they all leave the nest together, traveling in a compact mass and zealously guarded by the very pugnacious male. As the young grow, the compactness of the school slowly lessens until, when the young are nearly four inches long, the mass formation disappears and the young go about their business on their own responsibility. While guarding the young, the male dogfish will attack anything that threatens the precious mass of youngsters. I have had the parent attack nets, rakes, sticks—anything I thrust toward the ball of young; a vicious attack, a strike at the intruding object, and a dash away to a distance of about six feet; a swift turn and another vigorous attack. During this performance by the old fish, the school breaks up in every direction, the young going to the bottom and scurrying toward deeper water under the protection of the vegetation. The food consists entirely of animal matter, varying between fish and crayfish at different seasons of the year, the late summer and fall finding the latter the dominant food. Among the fish, over and above many species of minnows, which I have taken from the stomachs are: *Lepomis pallidus*, *Lepomis gibbosus*, *Micropterus salmoides*, *M. dolomieu*, *Perca flavescens*—in fact, small specimens of all of the game or food fishes. Economically, then, inasmuch as the dogfish is never considered as of any food value in this region, it must be classed as a species destructive of game fish. Commercial fishermen always destroy every gar and dogfish they catch in their nets. The species attains considerable size, specimens that I have taken weighing as high as eight pounds.

## Order ISOSPONDYLI

### Family SALMONIDAE

#### 3. *Coregonus albus* (Le Sueur). Whitefish.

The whitefish is not a native of the inland lakes, and is included in this list because an attempt was made to introduce the fish, an effort which was only temporarily successful. In 1887, according to the report of the game warden department, 350,000 whitefish were planted in Oconomowoc lake. Nothing was seen of the fish for several years. About 1891 whitefish were

caught in winter by fishermen working through the ice, along with ciscos, from which they apparently were not distinguished. The weight at this time was four and five pounds. During the few years following, the original planting was entirely caught out, and there is no evidence of the whitefish ever having reproduced while in the lake. The writer has examined many thousands of ciscos caught in this lake during the winters but has never seen any sign of the whitefish. It is concluded that the species has become extinct. The inland lakes of southern Wisconsin are not of sufficient depth or coldness to accommodate whitefish, the thermocline forcing the deep (and therefore cold) water species into near-surface water of a temperature too warm for their existence.

4. *Leucichthys artedii* (Le Sueur). Cisco.

The cisco, a deep water fish, is confined to those bodies of water having a considerable depth. I have taken ciscos from the following lakes: Lac La Belle, Fowler, Oconomowoc, Okauchee, North, Pine, Nagawicka, Upper and Lower Nashotah, Upper Nemahbin, Golden and Dutchman's. Of these, La Belle, Oconomowoc, Okauchee and Pine contain the species in the greatest abundance at the present time. Lower Nashotah and North lake ciscos average the largest in size, while Pine lake is literally full of small ciscos averaging not over a fifth of a pound. In the other lakes mentioned, the numbers are not great. When cisco fishing first began, the average size of the catch was somewhere around two and a half pounds each; today a cisco weighing a pound causes a sensation and is an object of admiration. As a result of observations during winter fishing over a long period of years, I come to the conclusion that Oconomowoc lake alone yields not less than 40,000 ciscos each winter.

The cisco normally inhabits the deepest and coldest parts of the lake. With the formation of the thermocline, however, the fish are forced up from the depths into water uncongenially warm. During exceptionally hot summers the fish are forced into water so warm that they can not adjust to it, the result being "epidemics" of dead fish, during which seasons literally thousands of ciscos perish in each of the lakes so affected. I have witnessed this in Oconomowoc, Pine and Okauchee lakes during the last six years. The summer of 1925 witnessed such an epidemic in Okauchee lake. On September 1 I counted 72 dead ciscos on ten feet of shoreline! The entire lake shore was strewn with dead fish, and after a careful survey, an average of two and a half fish per foot of shoreline was estimated. Since Okauchee has 8.1 miles of shoreline, it is estimated that on that date there were no less than 116,700 dead ciscos on Okauchee shores. The epidemic lasted for about six days, which gives some idea of the toll taken of the species. During the winter, when the thermocline does not exist, ciscos are normally caught in water 45 to 55 feet deep.



Spawning occurs in the fall, usually early in November, at which time the fish come into the shallow water along the shore or ascend the rivers to lay their eggs. Development follows very slowly, the young fish hatching sometime early in the spring, probably just prior to the breaking up of the ice. The young ciscos go immediately into deep water. The food consists almost entirely of plankton organisms, principally Cyclops, Daphnia, Diaptomus, Bosmina, Chydorus, rotifers and other organisms of a similar nature, as well as large numbers (in one case 376) of *Sayornis albipes* larvae. From an economic point of view, the cisco is a valuable food fish, particularly in the winter when the meat is firm and solid. Every effort, including the artificial propagation of the species, should be exerted to save these fish which are rapidly nearing the point of extermination. While the fish remain in deep water they have but few natural enemies; when they come into the shallower regions they are preyed upon voraciously by large pickerel (*Esox lucius*) and to a lesser extent by the gar (*Lepisosteus osseus*). 5. *Oncorhynchus tshawytscha* (Walbaum). California Salmon, or Chinook.

Like the whitefish, this fine species was introduced into Oconomowoc lake, but without success. The state fish commission reports show that in 1877, 4,800 fingerling California salmon were planted in this lake, and in 1879, 1,500 somewhat larger individuals were liberated in Nagawicka lake. Some of the fish were caught in the years immediately following, but the fish never reproduced and are now entirely extinct. The lakes are not cold enough to accommodate these fish, so that such transplantations are utterly fruitless.

6. *Salmo sebago* (Girard). Landlocked Salmon.

In 1879 the reports of the state fish commission at Madison show that 12,000 of these fish, in fingerling size, were planted in Nagawicka lake. Like the above species a few were caught shortly after the transplantation occurred, these weighing in the neighborhood of a pound to a pound and a half, but the species failed entirely to establish itself and quickly became extinct.

7. *Salmo irideus* (Gibbons.) Rainbow Trout.

The rainbow trout is not a native species in southern Wisconsin, but, notwithstanding this fact, the transplantation of the fish into the suitable trout streams of the county has resulted in the firm establishment of the species. Planted in such admirable streams as Rosenow's creek, flowing into Lac La Belle on the east, and Scuppernong creek farther south, the rainbows have bred and successfully maintained themselves amid the water-cress beds and the clear, cold spring water. Traveling down stream, the fish have entered various lakes, so that at least two—Lac La Belle and Dutchman's—contain the species in some numbers. I believe that I have taken the record rainbow for the county: a fish weighing four and three-quarters pounds, from Dutchman's lake, August 29, 1912. Since then many

smaller specimens have been taken from that lake. The seining of Lac La Belle for carp has revealed the presence of many fine rainbows in that lake. So far as I can see, the planting of the fish has in no way altered their breeding habits. Those fish that are in the lakes have been repeatedly seen going up the trout streams during the breeding season. The food of the fish consists almost entirely of insect life—flies, gnats, caterpillars, grasshoppers—anything that drops upon the surface is eagerly snapped up. Nothing need be said of the high quality of the rainbow as a food fish, and it is to be hoped that continued and enlarged plantings will proceed.

8. *Salmo fario* (Linn.). German Trout; Brown Trout.

Like the rainbow, an introduced species. Scuppernong creek, together with Waterville and Rosenow creeks, are the main sources of this very fine trout, which seems to do exceedingly well in its new environment. Dutchman's lake contains some very fine specimens up to three and three and a half pounds, and Lac La Belle likewise harbors some fine individuals. Under existing conditions, the brown trout seems to grow somewhat more rapidly than the rainbow, but tends to average about the same in ultimate size. I have records of several weighing between three and four pounds, taken mostly from the Rosenow stream, and a record of one "whopper" caught by Dr. F. F. Maccus, which weighed  $4\frac{1}{2}$  pounds. A fine fish, whose table qualities, however, hardly equal those of the rainbow trout.

9. *Cristivomer namaycush* (Walbaum). Great Lake Trout.

Another fish that was introduced in the early years of experimental transplantation. Like the California and Land-locked salmon, the lake trout was planted in lakes in the county. The records give no account of which lakes were stocked, but probably Oconomowoc and Nagawicka were the ones chosen. In 1877 and 1878 some 690,000 young were liberated. There is no evidence that any survived and it is certain that not one exists to-day. This is another well-intentioned experiment which went wrong because of the unsuitable lake conditions. These northern species can not withstand the warm water and relatively shallow conditions which exist in Waukesha county lakes.

10. *Salvelinus fontinalis* (Mitchill). Brook Trout; Speckled Trout.

Brook trout have been introduced into a great many spring fed streams throughout the county and there are few which meet the requisite conditions of cold, fast water which do not contain the species in some abundance. Scuppernong, Waterville and Rosenow creeks abound in brook trout from six to ten inches in length, and an occasional "monster" weighing over a pound and a half. I have records of three brook trout weighing over two pounds:  $2\frac{1}{4}$ ;  $2\frac{3}{8}$ ;  $2\frac{5}{8}$ . I can see no modifications of general habits of these transplanted fish. Their food, behavior, breeding habits, all are similar to those I have observed on the same species in their home environment. If these trout leave the streams and enter the lakes, I have

little evidence to show for it. Nets drawn in Lac La Belle have shown me only two brook trout, but this may be due to the smaller size of the fish and their consequent escape through the mesh of the nets. However, I am inclined to believe that the species shows less tendency to migrate than either of the other common trout—the rainbow and the brown.

#### Order APODES

##### Family ANGUILLIDAE

#### 11. *Anguilla rostrata* (La Sueur). Eel.

The eel is a rare fish in the Waukesha county lake district. During the years I have been gathering data on the fishes I have seen but five eels taken in the county, though there are records of an equal number at least that have been hooked, lost or seen. Four of the fish I have handled come from Lac La Belle, under the falls at the outlet of Fowler Lake. These fish measured: 2 feet 9 inches, 3 feet 6 inches, 3 feet 7 inches, and 4 feet 2 inches in length. Two were caught at night by men fishing for white bass in late May, worms as bait; the other two were speared. The fifth specimen came from the Oconomowoc river at the outlet of Lac La Belle and was speared. I have no doubt but that eels are more plentiful than these data seem to indicate, but these are all the records I have.

#### Order EVENTOGNATHI

##### Family CATOSTOMIDAE

#### 12. *Ictiobus cyprinella* (Cuv. & Valen). Big-mouth Buffalo; Buffalo-fish.

This, the commonest of the buffalos, is found in those streams tributary to the Rock River, in which water it is more common than in any of the Waukesha county streams. Found also abundantly in the Fox river, particularly south of the city of Waukesha. A fish of considerable size, often reaching ten pounds, it is taken in nets during carp seining and never, so far as I know, on hook and line. I have seen the fish taken from the Oconomowoc river near its entrance to the Rock, and in Lac La Belle, but never in numbers. My figures show an average of 91 carp (*Cyprinus carpio*) to 1 of this species. The food consists almost entirely of vegetable matter—algae, leaves and seeds of aquatic plants (*Potamogeton*, *Elodea*, etc.), together with a considerable number of zooplankton organisms, insect larvae (*Chironomus*) with mollusca represented occasionally by small *Sphaerium*. These forms are all sucked in and strained out of the water by the gill rakers which pass the mud and silt out with the water. Locally the fish are not looked upon with much favor as a food fish, there being plenty of bass and other high grade food fish available, but they bring a good price when shipped by commercial fishermen.

#### 13. *Ictiobus urus* (Agassiz). Round Buffalo; Mongrel Buffalo.

The various species of buffalo fish inhabiting local waters are not distinguished by local fishermen. This species is far less common than



either the preceding or the following, and I have seen it only twice, both times from Lac La Belle, into which it has undoubtedly come directly from the Rock river. These two seinings yielded 7 of the species weighing from 3 to  $5\frac{3}{4}$  pounds. The food and habits are almost identical with those of the preceding species, though a distinctly greater proportion of the food seems to be mollusca—Sphaerium, Valvata, Planorbis and Pisidium predominating.

14. *Ictiobus bubalus* (Raf.). Small-mouthed Buffalo; Quillback.

This is distinctly a deeper water species than either of the other two buffalo fish, and has been taken from the deep holes in the Fox river near Waukesha and in Lac La Belle. The species is much more common in the Rock river where conditions seem to be more congenial. A smaller species than either of the preceding, the small-mouthed buffalo averages about  $4\frac{1}{2}$  pounds within the region under discussion, though I have seen one specimen from the Fox river that weighed 13 pounds. The food consists of about equal parts of animal and vegetable matter, the former being algae, Potamogeton, Ceratophyllum, the latter entomostraca, crustacea (small crayfish occasionally, as well as zooplankton), and in one instance, bass eggs (*Micropterus salmoides*). The buffaloes are all considered valuable food fish, greatly preferred to carp (*Cyprinus carpio*) but none are eaten especially eagerly in this vicinity.

15. *Capriodes velifer* (Raf.). Quillback Carp; Silver Carp.

Not common within Waukesha county, but occurring in the Oconomowoc river between Lac La Belle and the outlet into the Rock river; the Fox river west of Duplainville and down the river to the southern county limits; and in Lac La Belle. A small species which, when caught in nets, is not distinguished by the fishermen from the buffaloes, and it has no value as a food fish, the average size being under 12 inches. Its food consists very largely of vegetable matter—fragments of aquatic vegetation and algae, with occasional insect larvae (*Chironomus*) and quite a variety of gastropod mollusks (*Planorbis*, *Physa*) and small clams, mostly young individuals. It is distinctly a shallower water form than the buffaloes.

16. *Erimyzon sucetta oblongus* (Mitchill). Chub Sucker.

The first records I obtained of this species, and for a long time the only records, came from the Menomonee river in the northeast corner of the county, a stream draining into Lake Michigan. Here the species is not uncommon and it was only in 1924 that I discovered the species in Fowler lake, the only other record I have. The fish is small in size; five inches is the longest individual I have taken, the majority being under four inches long. In the river habitat they prefer flowing water of not great depth, where they have the darter habit of maintaining their position on the gravelly bottom by means of the pectoral and pelvic fins, head upstream. In Fowler lake, however, I have seen no indication of this habit,

the fish behaving in normal minnow fashion. They are bottom feeders, taking in much silt from which the plankton organisms are strained and retained as food. Diatoms, algae, Sphaerium, small bivalves, Physa and Planorbis, insect larvae and an occasional insect form the chief items of food, the vegetable matter dominating to the extent of about 70%. Of no value as a food fish because of its small size.

17. *Catostomus commersonii* (Lacepede). Common Sucker.

A common sucker in the Oconomowoc, Ashippun, Bark, Muckwonago and Menomonee river systems, being almost wholly confined to these streams. In the rivers the fish attain a length of from 10 to 12 inches, rarely more, but I have taken specimens 13 and 15 inches long from Oconomowoc lake. Those individuals which inhabit the lakes of these river systems often ascend the streams soon after the ice goes out in the spring, and spawn on the riffles, usually about the middle of April. The young remain for the most part in the rivers, going down to the lakes only when they are nearly fully grown. That some of the fish spawn in the lakes is indicated by the presence of young fry taken in minnow nets along the shores of Oconomowoc, Silver, Golden, Keesus, Pine and La Belle lakes. The chief economic value lies in their being used as food for bass, pickerel and other valuable food fish.

18. *Hypentelium nigricans* (Le Sueur). Hognosed Sucker; Stone-roller.

This sucker is confined strictly to the rivers, and I have no lake records for the species. The Bark river contains the greatest numbers of these interesting fish, and I have taken them in the Oconomowoc river as well. They show a preference to swiftly flowing water, avoiding those reaches of the river where silty bottom or deep water slows up the current. Like the darters they come to rest heading upstream, the large pectoral fins acting as a brace against the current. Very fast of movement, when disturbed they dart off at great speed, but only for a very short distance, while the dark mottled coloration of the back acts as a protection, rendering the fish almost invisible against the mottled river bottom. The food consists almost entirely of animal matter, largely insects and larvae, with only a small proportion (6%) of mollusca, and 12% of vegetable material. Of no economic value.

19. *Moxostoma aureolum* (Le Sueur). Common Red-horse.

A very common sucker of the Rock river, the red-horse is found in all streams tributary to the rock, and only as far as dams prevent their distribution. Thus they are found abundantly in the spring in the Oconomowoc river as far as the Lac La Belle dam, where many are speared every year. The Ashippun river and the Bark river, together with the Scuppernong river also contain red-horse and the fish are caught in some numbers from all of these streams. They are used as food by many, but during the summer (August) when they can be caught on hook and line, the meat is soft and

of poor keeping quality. Though the average weight is about two pounds, I have taken specimens weighing  $3\frac{3}{4}$  and  $4\frac{1}{2}$  pounds. The smaller individuals are occasionally found in the stomachs of wall-eyed pike and pickerel, and less frequently in the black and green bass. While the species may prefer clear water and a gravel bottom, the fact that they are found in water rendered turbid by the activity of the carp, speaks for a wide range of tolerance if no actual impurities exist. They can not stand pollution.

20. *Moxostoma breviceps* (Cope). Short-headed Red-horse.

Somewhat less common than the preceding, though of the same distribution, this species is not separated ordinarily by local fishermen. I have taken the species in all of the rivers named for the preceding, but the fish are more numerous in Rock river and in the Rubicon river in Dodge county to the north.

#### Family CYPRINIDAE

21. *Cyprinus carpio* (Linn). German Carp; Leather Carp.

"The day will come when the people of the state (Wisconsin) will thank the men who have introduced and planted this extra fine species of fish (carp)." So said Dr. Lapham in a paper published in 1882. Since that time, this "extra fine" species of fish has spread to almost every lake in the county, and is in all the river systems. So abundant has it become in certain lakes (Lac La Belle) that periodic seining is necessary to save the game fish and their protecting weed beds. There is no mystery as to how the carp has become so widely distributed: young carp were formerly used as bait (being easily caught in the rivers) and being tenacious of life, the minnows left over were thrown overboard, to live and establish themselves. It is difficult to name a single lake in the county that does not contain carp. The only one of the larger lakes in which I have never seen a carp is Oconomowoc lake, on which I have lived for twenty-two summers. Yet Okauchee which flows into it, and Fowler into which Oconomowoc flows, both contain carp, and the rivers between are alive with them. The average size of carp in the county is from four to six pounds, though I have weighed specimens from Lac La Belle that went to 31 pounds, and the Rock river contains specimens up to 42 pounds. The fish prefer soft-bottomed lakes, in which they nose around, much like so many pigs. The result is the uprooting of the vegetation, the destruction of weed beds, and the dispersal of the game fish that habitually frequent such beds. Not only this but the water is muddied by the digging to such an extent that in many cases it is opaque. This sediment of course tends to settle over deposit-eggs, and many are destroyed. I had opportunity in 1924 to examine the entire fauna of a large lake as it was drained, and in a future paper I shall show just how the carp affects a lake.

Spawning is in late May or early June, the carp coming into the shallow waters and depositing their eggs in tremendous numbers on the shallow



water plants and roots of trees that may extend out into the water. Thus I have seen roots of willows so loaded with eggs that the roots themselves were invisible. There is a very high mortality among the eggs, many of them dying before gastrulation takes place. The young carp, like the old, are gregarious, and often come up into the shallow waters along the shore. I recall a school that tried to ascend the Oconomowoc river from La Belle. In a single dip with a net twelve inches in diameter, I scooped out 291 carp. Growth is rather slow; by the end of the first summer the fish are just approaching four inches. The food consists of a tremendous amount of bottom debris which is sucked in and the minute organisms strained out. The fish bite readily usually on such bait as clam meat and put up a very vigorous fight. A carp caught on a fly rod is about as good sport as one could ask for. As a food fish it is little used, though many of the farmers "put them up sour" as they are not bad. However, the damage they do outweighs their food value so far as local consumption goes, though the commercial seiners, catching anywhere from five to fifteen or twenty tons a year, make good money selling them outside of the state at eight cents a pound. A determined effort should be made to rid the lakes of the carp, and then to keep them out. This can be done if systematically undertaken.

22. *Carassius auratus* (Linn.). Goldfish.

Although, of course, an aquarium fish, many goldfish have been liberated in Oconomowoc and La Belle lakes, where they have established themselves, reproducing in considerable numbers. Two schools of large fish, weighing up to two pounds, exist in La Belle, and one school in Oconomowoc lake. That the fish are breeding successfully is indicated by the varying sizes of the individuals forming the schools, and by the presence of individuals under three inches in length. They frequent the deep water off the bars during most of the year, but spring (late April and early May) finds them up in the shallows, where they are quite a sight for a few days.

23. *Camptostoma anomalum* (Raf.). Stone-roller.

A very common minnow of the Ashippun, Bark, and Menomonee rivers, with a few of the species found in almost any gravelly stream. They avoid muddy or stagnant water entirely, being most abundant just under rapids of clear water. They attain a size of five inches, rarely more, though the average is not over four inches. In June the males of the species, in full nuptial coloration and adorned with tubercles over the entire body, can be seen carrying stones for the construction of the nest. Many small pebbles measuring up to  $\frac{3}{4}$  inch in diameter, are carried in the mouth upstream to a clear gravel area and deposited in a pile eighteen inches in circumference. In Bark river I have seen piles of nearly half a bushel above the nest. The work is done entirely by the males and it would appear that several work together on a single nest. The food consists entirely of

vegetable matter, mixed with a large amount of fine mud and silt, all of which is passed through the digestive system. Algae, diatoms, desmids and particles of larger aquatic plants are the principal food I have found. The species is hardy and makes very good casting bait. An inhabitant of shallow water, it apparently has few enemies among the fishes, though many are eaten by herons and bitterns.

24. *Chrosomus erythrogaster* (Raf). Red-bellied Dace.

One of the most beautiful of our fresh water fishes. The brilliant coloring of the male, together with the very fine scales, has confused the species in the local minds with trout, for which it is often mistaken. It is abundant only in the Ashippun river, but occurs sparingly in the Oconomowoc and Scuppernong rivers. In the Ashippun it is found over gravel bottom, in clear, running water and associated with *Notropis cornutus* and *Hybopsis kentuckiensis*. Breeding occurs late in May or early in June, and the male carries traces of his brilliant red belly late into the summer. The food consists entirely of entomostraca, algae and particles of aquatic vegetation, with an occasional *Hyaella* or *Gammarus*.

25. *Hybognathus nuchalis* (Agassiz). Silvery Minnow.

A very rare species, recorded only from the Menomonee river, and therefore found only in the Lake Michigan drainage area. Three specimens are all that I have taken. These came from water slightly muddy in quality, over a fine silt bottom, and with only slight current. Two specimens were examined for food, and showed an abundance of entomostraca, diatoms and algae (mostly *Spirogyra*) abundantly mixed with fine silt.

26. *Hybognathus nubilus* (Forbes).

Another rare species, found most commonly in the Scuppernong creek, where I have taken thirty-eight specimens. The water here is dark grayish brown in color due to a large amount of fine silt and muck in suspension. The bottom is soft, the water eighteen inches deep and normally with little current. The food seems to consist almost entirely of algae (*Spirogyra*, *Zygnema*, *Closterium*) with occasional entomostraca and small insect larvae. Nothing is known of the breeding habits.

27. *Pimephales promelas* (Raf). Fathead Minnow.

Like *Hybognathus nuchalis*, with which it is associated, this species is recorded only from the Menomonee river, where, however, it is extremely abundant. In this river it is the dominant fish species, and I have taken two hundred or more in a single sweep of a minnow net. It is most common in muddy water, and entirely absent from those parts of the river flowing over clear gravel. It is a bottom feeder, apparently grubbing in the soft bottom for insect larvae which form over 90% of its food. The species breeds in June, usually rather late in the month, the nests being shallow depressions near or under the banks. In this region the fish are characteristically infected with the small black cysts of a fluke probably *Diplostomum*.

*lum cuticola*, so heavily, in fact, that the fish often appear entirely black in color.

28. *Hyborhynchus notatus* (Raf.). Blunt-nosed Minnow.

One of the very commonest of the local minnows, found in nearly every lake and every stream. It shows little preference as to lake or stream habitat, but is distinctly more abundant in clear than in muddy water. It prefers the shallows, seldom venturing into water more than three feet in depth, and in the lakes, at least, is most often taken in water of a foot or eighteen inches in depth. The fish breed in June, though I have found females carrying eggs well into July. The eggs are laid on the underside of stones, cans, boards, or even pieces of paper provided the material is not actually buried in the bottom. How the eggs are deposited in this position I can not say. I have taken many nests along the shores of Golden and Oconomowoc lakes, with invariably one of the parents on guard, usually the male, as can be told by the group of tubercles on the snout. The eggs hatch in eight or nine days in water varying from 70° to 75°F. The fish are used abundantly as bait for bass, perch and silver bass.

29. *Semotilus atromaculatus* (Mitchill). Horned Dace; Chub.

Abundant in the Ashippun, Oconomowoc, Bark and Fox rivers, together with such of their tributary streams as afford congenial environment. Very gregarious, these minnows are found in schools of many hundreds, or at times thousands, in streams of moderately swift water and gravel bottom. During the warm weather, when the water level of the streams lowers, the minnows retire to the deeper holes, from which they are easily caught on hook and line with small angle worms as bait. Breeding occurs in early June, nests being constructed of much the same type as those of *Campostoma anomalum* with which they are frequently associated. This species, together with *Hybopsis kentuckiensis*, is the best bait available for bass, pike and pickerel, and many thousands are captured in the glass minnow traps for this purpose every year. So long has this been going on that the species is in danger of extermination in the not far distant future. A very game minnow, they feed on animal matter entirely, a large part of the food being insects which fall upon the water.

30. *Clinostomus elongatus* (Kirtland).

This exquisite fine-scaled minnow has been taken by me only in the Menomonee river, and is therefore represented only in the Lake Michigan drainage area. In this river it is associated with *Pimephales promelas* and *Hybognathus nuchalis*, inhabiting slightly muddy water of 18 inches depth and little current. The species is not common, and I have taken only 10 specimens. The food consists of entomostraca, with a few insects and insect larvae and quite a bit of algae (*Spirogyra*). The spawning apparently occurs in June as I have a specimen heavy with eggs taken June 14. It is rather surprising to find this species so far west; until I obtained my



specimens I believe that Michigan was considered the western limit of its range.

31. *Opsopoeodus emiliae* (Hay). Small-mouthed Minnow.

Rather an uncommon species, taken by me only in the Oconomowoc and Ashippun rivers. Small in size—usually under two inches—the fish often escapes notice, as it frequents water somewhat muddy in quality and of considerable depth. In the Ashippun the species inhabits the deeper holes over soft bottom, where the fish feed upon entomostraca and small crustacea such as *Hyaella*.

32. *Notemigonus crysoleucas* (Mitchill). Golden Shiner.

A species with a very peculiar distribution within the county. For a long time I knew it only from Washtub lake, where it is extremely abundant. In 1924 I found it in shallow weedy water along the shores of Lac La Belle, and in 1925 I took it from shallow water weeds in Oconomowoc lake. In Washtub, which is a small lake nearly choked with weeds, the species seems to be at its optimum. The fish reach a length of four inches or less, and are not particularly hardy if used as bait. A great variation in color exists locally. Those from Washtub are very dark with a brassy tinge, while those from La Belle are very light and show almost no trace of yellow. The food consists largely of entomostraca *Hyaella*, with a large number of young water-boatmen (*Corisa* sp.) and backswimmers (*Notonecta* sp.), and occasionally young leeches (*Placobdella parasitica*). Aquatic vegetation comprises about 20% of the food. Gravid females have been taken early in June and well into July, while spawning apparently occurs normally about the middle of June.

33. *Cliola vigilax* (Baird & Girard). Bullhead Minnow.

Locally common, but very circumscribed in distribution. I have taken the species in the Menomonee River, closely associated with *Pimephales promelas* and *Hybognathus nuchalis*, and in the Ashippun river in association with *Camptostoma anomalum* and *Catostomus commersonii*. The food consists of about equal parts of aquatic vegetation, entomostraca and occasionally mollusca, such as small *Physa* and *Planorbis*.

34. *Notropis cayuga* (Meek). Blunt-nosed Minnow.

A very abundant species in the Mukwonago river, and present to a much less extent in the Fox and Oconomowoc rivers. I have taken the species several times in Oconomowoc lake, but it is very rare in lakes. Usually found associated with *Notropis cornutus* and *N. whippelii*, it prefers gravel bottom, medium current and relatively shallow water, seldom being taken in water more than twenty inches deep. The food is largely entomostraca, though insect larvae and a little vegetable matter in the form of algae are often found in the stomachs. Although I know nothing of the breeding habits, it would seem that the species is a late breeder, as gravid females have been taken commonly in July and several as late as August 10. A good bait minnow.

35. *Notropis heterodon* (Cope). Black-striped Minnow.

Common locally in most of the larger lakes—Oconomowoc, La Belle, Golden, Keesus, Pewaukee, Pine—where the species goes in schools often numbering two hundred individuals. Seldom taken in streams, the only record I have being the Oconomowoc river below the outlet of Oconomowoc lake from which the fish may well have come. The Milwaukee Museum has specimens from Stonebank creek at Hartland. The fish feed almost entirely upon entomostraca, though I have found insect larvae and *Hyalella*, very small snails (*Physa*) and leech cases (*Placobdella parasitica*) in a number of instances. A hardy bait minnow, much used for silver bass fishing.

36. *Notropis blennioides* (Girard). Straw-colored Minnow.

Probably the most abundant minnow in all of the large, sand-and-gravel lakes. In such lakes as Oconomowoc, La Belle, and Pine it is the dominant shore minnow, present in incredible numbers. The species is gregarious and I have seen schools in Oconomowoc lake containing at least 5,000 individuals. They are commonly associated with *Fundulus diaphanus menona* and the young of *Lepomis pallidus*, *L. cyanellus*, *Perca flavescens* and *Ambloplites rupestris*. Spawning occurs along the shores in water from twelve to eighteen inches deep in late May and early June, usually under the protection of shallow water submerged vegetation. The standard small bait minnow of the region. I have found the fish in Oconomowoc lake often infected with large tapeworms (*Ligula* sp.). In August, 1925, I took a minnow 5 cms. long whose body cavity contained a *Ligulid* 6.2 cms. in length.

37. *Notropis hudsonius* (DeWitt Clinton). Spot-tailed Minnow.

Exceedingly abundant in Bark, Ashippun and Oconomowoc rivers; less so in the Fox river and its tributaries. To some extent found in Oconomowoc lake; rare in Okauchee, Pine, La Belle, and North. In the rivers, which seems to be its normal habitat, the species prefers clear water, and gravel bottom with not much current. It is associated with *Notropis cornutus*, *Hybopsis kentuckiensis*, and *Semotilus atromaculatus*. A hardy bait minnow, though very small in size, seldom reaching a length greater than 3 inches. While Forbes and Richardson feel that the species intergrades with *N. whippelii*, I can see no evidence within the region to bear out such a conclusion. To the extent of 80% the food is animal matter, being entomostraca, small crustacea, and occasionally young mollusca of any species that may be at hand.

38. *Notropis whippelii* (Girard). Silverfin Minnow; Lemon-fin Minnow.

The name used locally for these minnows depends on the season of the year and on the sex of the minnow in question. Extremely abundant in the Muckwonago river, and quite common in places in the Oconomowoc and Fox rivers. It is a swift water, clear gravel-bottom species, which avoids

heavy vegetation except for momentary protection. I have taken the species in Lac La Belle, where it is established and breeding. In rivers it is usually associated with *Notropis cornutus*, *Hybopsis kentuckiensis* and *Camptostoma anomalum*. A beautiful minnow, but not hardy enough for bait purposes.

39. *Notropis cornutus* (Mitchill). Common Shiner.

The characteristic minnow of Ashippun, Bark, Mukwonago and Fox rivers where it is exceedingly abundant. In the Bark and Ashippun rivers I have often taken a glass minnow trap so full of these shiners (as many as 277 in a single trap) that movement within the trap was impossible. The fish attain a large size, often reaching 6 and 7 inches, and are excellent, though short lived and tender mouthed bait. They are commonly used for clear water trolling, not for casting. They prefer clear water (in fact they cannot survive in muddy water), gravel bottom with protecting weeds near at hand, and some current. As a result of excess bait being thrown overboard, the species is sometimes found established in lakes—Oconomowoc, Pine, North (very abundant), and Okauchee. The food is about equally divided between entomostraca, crustacea and insect larvae as animal food, and algae, slime, and particles of aquatic plants on the vegetable side.

40. *Notropis atherinoides* Raf. Shiner.

Taken by me only in the Menomonee river, where it is not very common. Here it was associated with *Pimephales promelas*. The food consists almost wholly of animal matter, largely insect larvae, but many adult insects which have fallen on the surface are eagerly snapped up. I have found these fish likewise infected with a species of Ligula.

41. *Notropis rubrifrons* (Cope). Rosy-faced Minnow; Skip-jack.

The only place I have taken the species is in the Mukwonago river, where it occurs in large numbers at certain seasons of the year. It would appear that the species comes up from the Fox river in late spring, returning to that river again about October. In no other way can I explain the complete disappearance of this species which is so common in the Mukwonago during the summer. Inhabiting water two feet or more in depth, the species is often eaten by bass (*Micropterus salmoides*) and pickerel (*Esox lucius*). A very interesting minnow, about which little is known.

42. *Rhinichthys atronasmus* (Mitchill). Black-nosed Dace.

This peculiar little minnow which, because of the profusion of small black pigment spots looks as if it were heavily infected with cysts of *Diplostomulum cuticola*, has been taken only from the Lake Michigan drainage in the Menomonee river. Here it is quite common, associated with *Pimephales promelas* and *Clinostomus elongatus*. It prefers rapid, clear water, and gravel bottom with some vegetation. The mouth is rather sucker-like and the food consists largely of vegetable matter, together with what entomostraca and small crustacea and insect larvae may come with it.



43. *Hybopsis kentuckiensis* (Raf.). Chub; Horny-head.

One of the most abundant fish in the Ashippun, Bark and Mukwonago rivers, together with their tributary streams. Formerly abundant in the Oconomowoc river, but the numbers here are now greatly reduced. This fine minnow, reaching a length of 6 and 7 inches, is, together with *Semotilus atromaculatus*, to which it is superior for the purpose, the best casting minnow, and tens of thousands of them are captured yearly for the purpose. I personally know two guides who have taken not less than 600 of these chubs a week for five months a year for more than forty years, from the Ashippun river, and still the fish are abundant. This is to say nothing of dozens of other bait catchers who also frequent this productive stream. The fish breed in May and June, spawning over clear gravel in which a nest is constructed of pebbles. I have frequently seen several females spawning in the same bed, the construction of which is undertaken by the horny-headed males. The chubs bite readily on hook and line, by which method they formerly were captured for bait. However, the glass minnow trap has superseded this method, and hundreds can now be caught in an hour without injury to the fish.

## Order NEMATOGNATHI

## Family SILURIDAE

44. *Ictalurus punctatus* (Raf.). Channel-cat.

An introduced species which is in the process of establishing itself. Since the reclamation service along the Mississippi has been functioning, many of this species have been shipped in and planted in various lakes. Thus Oconomowoc received about 700 fingerlings in August 1925, and other plantings have been made in Nagawicka, Golden, Fowler and La Belle. In 1909 ten fish of this species, weighing about half a pound apiece were planted in Nagawicka lake. In July, 1923, one was caught in that lake weighing just under 5 pounds. I have no evidence to show whether or not the species is breeding.

45. *Ameiurus natalis* (Le Sueur). Yellow Bullhead.

The characteristic bullhead of the Rock river and its tributaries, as well as of most of the larger lakes. I have taken the species in Fowler, Oconomowoc, La Belle, Okauchee, Pine, Nagawicka, both Nashotahs and Nemahbins, Pewaukee, and Ashippun lakes. A lover of soft bottom and heavy weeds, usually Potamogetons. Usually about  $\frac{1}{2}$  to  $\frac{3}{4}$  of a pound in weight, an occasional individual weighing 2 pounds is taken. The species seem to do equally well in clear and muddy waters, lakes or rivers. The fish are for the most part inactive during the day so far as feeding is concerned, but they bite well as dusk approaches, and far into the night. The fish spawn in the lakes in heavy banks of weeds; in the rivers usually up under overhanging banks or at the entrance of deserted muskrat

burrows. Their food is anything that may come to hand: they feed almost wholly on animal matter, alive or in any stage of decomposition, fish, crayfish, and any refuse they can find. Notwithstanding, an excellent pan fish.

46. *Ameiurus nebulosus* (Le Sueur). Brown Bullhead.

By far the least common of the native bullheads, taken by me only in Oconomowoc, Ashippun and Laura lakes, in the Oconomowoc river near its entrance into Rock river and in the Pewaukee river near its entrance into the Fox river, and only sparingly here. They seldom attain a length of more than fourteen inches, and are not ordinarily separated from the preceding species by fishermen. A good table fish, whose diet is entirely animal food, but much less of the scavenger type.

47. *Ameiurus melas* (Raf.). Black Bullhead.

This is an abundant species in all of the soft-bottomed lakes and muddy streams. It is characteristic of small ponds. I have caught dozens in the Skidmore ponds and the small pot-holes near Okauchee lake. They live among submerged vegetation, and a characteristic sight of June and July is the little balls of young bullheads herded about by the adult, up near the surface of the water and along the shoreline. The nests are made either at the base of the weed beds, or under the overhanging banks. The old fish are very solicitous about their young, and attack any small fish that approaches the family school. On being disturbed the little black babies disappear into the weeds in every direction, but soon come together again in deeper water. The smallest of our bullheads, seldom exceeding 6 or 8 inches, and hence of little food value.

48. *Leptops olivaris* (Raf.). Mud-cat.

Like *Ictalurus punctatus*, the mud-cat has recently been introduced from the Mississippi overflows and is thriving in Nagawicka and Oconomowoc lakes. There are, apparently, only a few of these large catfish in the lakes, and I have no evidence of their spawning. One of these fish, weighing 16 pounds, was caught on August 7, 1923, in Nagawicka lake, the bait being "night-crawlers."

49. *Noturus flavus* (Raf.) Stonecat.

I have taken this little fish in two localities: the headwaters of the Fox river near Lannon, and the Oconomowoc river at Stonebank. The stonecat is a fish of clear water and fast current exclusively, living under stones in the midst of the fastest riffles and rapids. Habitually headed upstream, the fish are very quick in their movements, and escape almost miraculously under a minnow sein. The food seems to be entirely animal matter, largely insects and Chironomus larvae, though small mollusca are sometimes found in the stomach. I have twice found in the stomach a considerable number of Planarians.

50. *Schilbeodes gyrinus* (Mitchell). Tadpole Cat.

This little stonecat is, like the members of the entire group, an inhabitant of clear rapid water, where it is associated with *Noturus flavus* and various darters. I have taken it only in the Oconomowoc river at Stonebank, where it lives in the riffles under stones, cans, logs or any other available covering. The food is entirely animal matter, similar in composition to that of the preceding species. That breeding occurs late in May is indicated by the fact that while I have taken many gravid females before May 15, I have never seen one after May 25.

51. *Schilbeodes exilis* (Nelson). Slender Stonecat.

Also from the Oconomowoc river at Stonebank, and twice I have taken the species in the Mukwonago river. The rarest of the genus within our limits. Food and habits apparently very similar to the preceding species.

52. *Schilbeodes miurus* (Jordan). Brindled Stonecat.

Strangely enough, this species, while inhabiting very similar waters, has never been taken by me in association with either of the preceding. My specimens have come almost entirely from the Menomonee river, and for a long time I thought the species was limited to the Lake Michigan drainage area. But in June, 1925, I took two specimens from the very headwaters of the Fox river near Lannan. The fish inhabit running water but seem to avoid the fast current preferred by the two preceding stonecats. They likewise live largely under stones, logs or other protecting objects but seek water of a somewhat greater depth, two feet as against a foot or often less for the other species. They also show a somewhat greater tolerance for muddy water but are never found in water that approaches opaqueness. The food is, again, entirely animal, largely larvae of Chironomus, Hydropsyche, Aconeura and various species of mayfly, and small dragon-fly nymphs. The stonecats are not separated by natives and are all grouped together as "young bullheads."

## Order HAPLOMI

## Family UMBRIDAE

53. *Umbra limi* (Kirtland). Mud Minnow.

An abundant inhabitant of the innumerable small, muddy vegetation-choked ponds scattered throughout the region, and also in streams of a similar character. Among the latter I have taken the species from the headwaters of the Fox river in association with *Esox americanus*, *Schilbeodes miurus*, *Catostomus commersonii* and the crayfish *Cambarus propinquus*. In this stream it provides one of the chief foods of the grass pickerel. In the ponds it is most frequently associated with *Ameiurus melas*. No water seems too foul or too stagnant for these fish and no ordinary amount of drying up of ponds during a hot dry summer seems to exterminate them. They seek refuge in the soft muck of the bottoms, often completely burying



themselves in the ooze. Their tenacity of life is unique among our fishes, in spite of which they are never used locally as bait, presumably because of their dark color. The food is very largely aquatic plant material, duckweed (*Lemna*), particles of *Elodea*, *Ceratophyllum*, etc., together with any minute animal life that may be attached to this growth. Thus I have found particles of *Hydra* sp. in the intestine, probably off of *Elodea*. They spawn very early, probably as soon as the ice goes off the ponds, as I have no gravid females later than April 12. In the Fox river I have never seen a mud-minnow more than 3 inches long, while in the ponds near Okauchee lake I have taken them  $5\frac{1}{2}$  inches in length. Generally known as "young dogfish" locally.

#### Family ESOCIDAE

##### 54. *Esox americanus* (Gmelin). Grass Pickerel; Little Pickerel.

Found in only one locality in the county, the headwaters of the Fox river in the vicinity of Lannan. It was quite a surprise to find this little pickerel so far north as this is one of the most northern records, but in the northern waters of the Fox river and until the river becomes about twenty feet wide, this pickerel is the dominant and characteristic species. In this region the water is muddied by carp activity, normally but two feet deep, slow and sluggish, but not stagnant, and the bottom is a mixture of sand and mud. Here the pickerel lives on mud minnows and crayfish, and attains a length of 9 inches, though I have taken few so large. The fish spawn in typical pickerel manner, coming up into the overflowed marsh during the spring flood, to lay their eggs in the shallow water. The young pickerel are about two and a half inches long at the end of the first summer, their food consisting of young crayfish (*Cambarus propinquus*) which are unusually abundant there, and darters and small minnows (*Notropis hudsonius*, *N. cornutus*, *Umbra limi*) with an occasional *Physa* and *Gammarus*. The fish are so small as to be of no economic value.

##### 55. *Esox lucius* (Linn). Great Northern Pike; Pickerel.

The common pickerel of the region. Very abundant in all of the lakes and less so in all of the rivers, except during the spawning season. The greater part of the summer is spent just off of the sand bars in water 18 to 25 feet in depth, where the voracious fish lie in the Potamogeton beds and gorge themselves on any passing fish of convenient size. Feeding is almost entirely during the daytime and only very seldom is one caught at night. The food is normally fish, all species of minnows and small Centrarchidae included, with crayfish varying the diet during late summer. They grow to very great size, the largest I have weighed was  $27\frac{1}{2}$  pounds; it was caught in the Oconomowoc river near Fowler lake. I have many records of fish weighing between 15 and 18 pounds, but each year sees fewer of these large specimens caught. Newspapers published during the

early summer of 1925 a photograph of 16 pickerel with a total weight of 112 pounds, caught in Muskego Lake, but such catches are unusual, to say the least. Okauchee lake probably has more pickerel than any other lake in the county, and not long ago catches of 15 or more a day were standard. The larger pickerel do some damage by their destruction of game fish. Small bass, sunfish, silverbass, perch, suckers and cisco are preyed upon. I have taken three cisco weighing nearly half a pound each from stomachs of pickerel weighing 8 pounds. The pickerel spawns soon after the ice goes out, passing up into the marsh overflows to deposit their huge quota of eggs. These eggs hatch in about two weeks, the young fish spending the summer in the weed beds along the lake or river shore. By the end of the summer they attain a length of 8 or 9 inches, and have worked out into deeper water near the edge of the bars. A great game fish, that takes any good minnow bait readily and puts up a stubborn fight. Not particularly prized as a food fish because of the many bones.

56. *Esox immaculatus* (Garrard). Muskallunge.

No longer present in the county, there seems little doubt but that this greatest of freshwater game fish formerly occurred in the Fox river, which seems to have been a considerably larger river not very long ago. Dr. P. R. Hoy reports the species from this river, with a specimen weighing 40 pounds, caught in 1877. It is certain that the species has been extinct within the region for at least thirty years, in spite of reports which reach me constantly. Every large pickerel is suspected of being a "musky."

#### Family POECILIIDAE

57. *Fundulus diaphanus menona* (Jordan & Copeland). Menona Top-minnow.

This is the most abundant of all the Killifishes in the region and is characteristically a lake species. All of the larger lakes, those with gravel and sand shores, such as Keesus, Oconomowoc, La Belle, etc., harbor great numbers of these fish. They are distinctly shallow water forms, seldom entering water more than twenty inches in depth, and are commonly associated with *Notropis blennioides*, *Labidesthes sicculus*, and young Centrarchidae. Of the three species of Killifishes in the region this is the least "top-water" of the group. They remain well toward the bottom, feeding on crustacea, entomostraca and some insect larvae, and only occasionally come to the top to get a gnat or fly that has fallen on the surface. They spawn very late, often not until late in July, though they seem ready to burst with eggs by late June. An excellent bait minnow seldom more than  $2\frac{1}{2}$  inches long.

58. *Fundulus dispar* (Agassiz). Top-minnow.

This interesting killifish has been taken by me only in the Mukwonago Millpond, at the town Mukwonago. Here the species seems to be abun-

dant. The water of the millpond is dark due to much sediment in suspension, and has very soft mucky banks and reedy shores. Among these reeds this species is seen swimming just under the surface, or even sometimes with the dorsal fin out of water, feeding largely on tiny insects that chance to fall in the water. They are rather slow in their ordinary movements, but zig-zag away rapidly if disturbed, usually to return very shortly to the spot they left.

59. *Fundulus notatus* (Raf.). Top-minnow.

Next to *F. diaphanus menona*, the commonest of the killifishes. They frequent rivers and streams in preference to lakes, and I have taken them in Battle creek, and in all of the river systems except the Menomonee. They prefer slowly flowing water, and do not seem worried by sediment in suspension. Like the preceding species, this top-minnow remains constantly just under the surface, and when disturbed it zig-zags wildly, but it does not descend. Yet their food habits are in striking contrast to the preceding: about 75% of the food is vegetable matter, almost wholly filamentous algae, *Spyrogyra*, and *Zygnema* predominating. The remainder of the food is mostly insects picked from the surface. They spawn late, seemingly carrying nearly mature eggs for several weeks. I have taken gravid females from June 10 to July 8. One of the stable foods of the small-mouth bass (*Micropterus dolomieu*) that inhabit the rivers.

Order ACANTHOPTERI

Family GASTEROSTEIDAE

60. *Eucalia inconstans* (Kirtland). Brook Stickleback.

The characteristic inhabitant of small, weed-choked creeks, so heavily overgrown with brush, usually willows, as to be almost invisible. In such little streams, tributaries to the Scuppernong river and creek of the same name particularly, this pugnacious little fish builds its nest, rears its young, and lives its life. This is the only fish here that actually builds a nest, in the usual sense of the word. This nest, made of tiny twigs and branches of water plants, is almost round in shape, and is well hidden in the dense aquatic vegetation. The fish guards the nest vigorously, and will strike at anything that intrudes on the premises, including the finger if it is advanced slowly. The food is largely insect life, over 50% being small non-aquatic insects that fall into the water. An interesting variation in the number of dorsal spines exists among the sticklebacks of Scuppernong creek particularly. While 5 is the typical number, both 4 and 6 occur. Out of 100 fish examined, 13 had 4 spines, 69 had 5 spines, and 18 had 6 spines.

Family ATERINIDAE

61. *Labidesthes sicculus* (Cope). Brook Silversides; Top-water.

In southern Wisconsin this is characteristically a clear-water lake species, seldom found in streams. Especially abundant in Oconomowoc



lake but common also in Fowler, La Belle, Pine, the Nashotahs and Nemahbins, North, etc. Occasionally taken in the Oconomowoc and Bark rivers. Together with *Fundulus notatus* and *F. dispar* the most persistently "top-water" minnow. They inhabit the upper foot of water normally, varying in their distribution with day and night and with the seasons as to whether they are littoral or pelagic. Very gregarious, they travel in large schools, and may be seen leaping out of the water after insects on the surface. The fish breed in May, spawning in the shallow water along the lake shore, and the eggs hatch in from 8 to 9 days. The young fish travel out to assume a position over deep water, and here many fall prey to small-mouth bass (*M. dolomieu*) cisco (*L. artedi*) and gar (*Lepisosteus osseus*). The food is very largely animal matter—entomostraca, rotifera (Anuraea), *Mysis relicta*, and occasionally a considerable amount of insect material (dipterous larvae). An interesting point to be noted is that the fish live for only fifteen to seventeen months: they die during the summer following their one and only spawning. Of no use as a bait minnow, and usually carefully replaced by fishermen who uniformly believe them to be young ciscos.

#### Family CENTRARCHIDAE

62. *Pomoxis annularis* (Raf). White Crappie; Silver Bass; Strawberry Bass; Calico Bass.

Less common than the following species, the white crappie is never distinguished from the darker species by local fishermen, who believe it a color phase of the latter. It is found in nearly all of the larger lakes, and in some of the smaller, such as Laura, showing no particular aversion to muddy water or soft bottoms, though it is more common in lakes with sand and gravel beds. It is a deep water species, living off the bars in 15 to 30 feet of water, and frequenting the Potamogeton beds. The young of the year are found in the shallow water weeds along the lake shores, and to some extent up the streams. They bite readily on small minnows (*N. blennius*) and are a high grade pan fish. I have taken this species in Neosha Millpond, Dodge County, just over the Waukesha county line, weighing  $3\frac{1}{2}$  pounds.

63. *Pomoxis sparoides* (Ladepede). Silver Bass; Crappie; Strawberry Bass; Calico Bass.

By far the most common of the silverbass in Waukesha county, inhabiting nearly all the lakes, whatever the size, though absent from the small ponds. Like the preceding, an inhabitant of the deeper water and the submerged vegetation. Here they feed voraciously on small minnows of many species, and young of perch, sunfish, pumpkinseed and occasionally of bass. The fish spawn during April, rarely carrying their eggs as late as May 5, and, like the preceding, the young are found along the lake shores

where they attain a length of just under two inches by the end of the summer. During the winter the fish bite in water 6 to 10 feet deep, and thousands are caught in Oconomowoc, Pewaukee, Okauchee and other lakes where ice fishing is practiced. The best bait is any of the shore minnows of small size, and rarely are they caught on angle-worms. An excellent pan fish, not as large, however, as the white crappie. These fish seldom attain a weight of over a pound, half a pound being normal size.

64. *Ambloplites rupestris* (Raf.). Rockbass.

An abundant species in every lake and in all of the rivers, less frequently taken in the smaller creeks. The rockbass seems to prefer the shallow water, though occasionally taken from the weed beds off the edges of the bars. They prefer weeds as their environment, and are commonly caught in the midst of heavy masses of Potamogeton. They spawn in the shallow water along the shore, often among rushes, where a slight depression is made in the sand or gravel, the adults keeping guard until the young hatch. The young rockbass is found in the shallow water weeds all summer, attaining a length normally of hardly more than an inch by fall. These are handsome little fish, with a coloration entirely different from that of the adult, being heavily mottled with very large pattern. The food is composed of about equal parts of insects, fish and crayfish, the young of the latter being the dominant food during the late summer and fall. They bite on almost any bait, worms, minnows, chub, or spoonhook, but are not game fighters. While they are really a very good pan fish, they are looked upon with distaste by local fishermen because of an entirely mythical infection of "grubs." They are, however, often parasitized rather heavily with the cysts of (?) *Diplostomulum cuticola*, as are the perch, which, notwithstanding, are regarded as an excellent table fish.

65. *Chaenobryttus gulosus* (Cuv. & Valen.). Warmouth Bass.

A rather uncommon sunfish, which is not ordinarily separated by local fishermen from the rockbass, which it somewhat resembles. A fish of the smaller lakes—Laura, Skidmore ponds, Genesee—it prefers soft, muddy bottoms to sand or gravel, and is tolerant of dirty water. It inhabits the dense weed beds of these lakes, feeding upon insects and small fish, and to a much less extent upon crayfish. It bites readily upon worms or minnows (*N. blennius*), and puts up about the same sort of fight as the rockbass. It reaches a length of about 8 inches, 6 inches, however, being nearer the average size. Not highly ranked as a pan fish because of its small size and resemblance to the ill-favored rockbass.

66. *Lepomis cyanellus* (Raf). Logfish; Green Sunfish; Blue-spotted Sunfish.

An abundant inhabitant of rivers, and to a less extent of lakes, though quite common in lakes of muddy rather than clear water. Weeds are essential to their habitat, and Potamogeton and Ceratophyllum afford

protection in most of the river systems. I have taken the species, which is common, in all the rivers except the Menomonee, where it is absent. Of the lakes, the smaller bodies of water like Skidmore ponds, Laura lake and similar ponds, have their logfish in large numbers, and they also occur to a lesser extent in clear lakes, Oconomowoc, Lower Nashotah, as well. In these latter, however, the fish seem not to attain so large a size. In Oconomowoc lake, I get a great many very small logfish in the shore weeds, yet large ones are rare. They attain a weight of a quarter of a pound or a bit more in the Oconomowoc and Fox rivers, but are not prized as a pan fish—for no particular reason it would seem. The food consists of any animal life that happens to be at hand—fish, crayfish, insects, larvae, mollusca. They bite readily on worms, but rarely on minnows, and put up a fight about equal to that of a goodsized rockbass. The fish spawn in June and July, making shallow depressions in the shallow water near the shore—often in rushes. Here the old fish bravely defends its nest against intruders. So strong is the defense reaction that I frequently have caught the fish on the nest with no other equipment than my hands. The eggs are whitish, and very sticky, lying in the nest in a mass. They hatch in 7 to 9 days.

67. *Lepomis euryorus* (McKay). McKay's Sunfish.

The rarest of the sunfish, known to me only from three specimens taken in Oconomowoc lake, on three different occasions, and always at night. Whether this is significant or not I can not say, as the habits of the species are but little known. These fish came from the north shore of the lake, in water less than a foot deep, over gravel bottom, and were taken in a minnow seine along with *Microperca punctulata* and *Labidesthes sicculus*. The largest specimen measures  $2\frac{1}{4}$  inches long.

68. *Lepomis humilis* (Girard). Orange-spotted Sunfish.

This tiny little sunfish is also rare in Waukesha county, and has been taken by me only from the headwaters of the Fox river at Lannon where it is associated with *Esox americanus* and *Umbra limi*. My largest specimen,  $2\frac{3}{4}$  inches long, was a male in full nuptial coloration, taken July 7, 1920, and is one of the most beautiful of our local fishes. I have not taken the species since this date, and a total of only five specimens has come to hand. The food consists of about equal parts of vegetable and animal matter, being composed of bits of Ceratophyllum, Potamogeton and Elodea, with some algae, together with entomostraca, insect larvae, a few tiny mollusca, and some very small crayfish (*Crambarus propinquus*). I know nothing of its breeding habits. The fish is so small as to be of no economic importance.

69. *Lepomis incisor* (Cuv. & Valen.). Bluegill; Sunfish.

Abundant in all the lakes and streams in the county, and by far the commonest of the true sunfish. In the lakes they are found in deep and



shallow water, the former being the large adults, the latter young individuals ordinarily not sexually mature. The fish are gregarious, inhabiting the heavy off-bar weed beds in association with *Micropterus salmoides* the silverbass (*Pomoxis sparoides*) and pickerel (*Esox lucius*). They vary greatly in coloration, depending upon the character of the water they inhabit, those coming from muddy water being very dark. Bluegills weighing a pound are frequently caught, and the species is highly prized as a pan fish. They are very game fighters, utilizing their width to the utmost to resist the efforts of the fisherman. The food is largely animal matter. The young fish live mostly on entomostraca and bits of leaves of Potamogeton and other aquatic plants, while the adults eat fish, crayfish, small mollusca, insect larvae and often insects which fall upon the surface of the water.

70. *Lepomis gibbosus* (Linn.). Pumpkinseed.

This is distinctly a fish of the rivers and streams, and only to a slight extent of the lakes. In the latter they are most frequently found near the mouths of the rivers, from which they probably came. They are also found in the smaller ponds, Skidmore and Okauchee ponds. The fish show a decided preference for weed beds in soft bottom, usually muck, and are consequently very tolerant of dirty water. They are only to a slight extent gregarious, and have a more general distribution through the streams than do the preceding species. They prefer deeper water, and seek refuge in holes in the stream bed. Vegetation is also a requisite of their environment and much of their time is spent in the shade of aquatic plants or overhanging banks. They breed in June, nesting in the shallows along the shore where a nest is excavated in the bottom, always amid vegetation, and here the male valiantly guards the eggs. The young leave the nest almost at once, and no further parental care is displayed. The food is essentially like that of the preceding. Their size is a bit too small to make them a choice food fish, as they seldom exceed 5 or 6 inches in length.

71. *Micropterus dolomieu* (Lacepede). Small-mouth Black Bass; Red-eye.

This is the gamest of all the local fishes, the best fighter known. It is abundantly distributed throughout the county, but is decidedly a fish of clear lakes though it is also found in muddy streams. The factor which determines the persistence (if not the existence) of the red-eye in a lake is gravel bars. While food may be abundant and water conditions ideal in a lake, if gravel bars are not present neither is the red-eye. These bars are essential to their breeding habits, and the breeding habits of a fish, far more than the food habits, determine whether a species can survive in a given body of water. The red-eye occurs in most of the larger lakes, and is conspicuously absent from the following: Golden, Ashippun, Genesee, Pewaukee, Henrietta, Dutchmans, Otis and other small ponds. The

fish inhabit the deeper water off the bars after the breeding season, but are not as dependent upon weed beds as is the next species. On still, hot days in mid-summer one often sees these fish at the surface, breaking water in quest of insects of all sorts that have fallen upon the surface. Thus I once took 8 honey bees from the stomach of a red-eye caught on a dry fly in the middle of Oconomowoc lake when the fish were very evidently "up." The species is very voracious and largely piscivorous during most of the summer, but toward fall the food changes to crayfish of which they are inordinately fond. During September and October the stomachs are packed with crayfish, often as many as 6 or 8 in a single alimentary canal. They bite well on chubs (*H. kentuckiensis* and *S. atromaculatus*), shore minnows (any species of *Notropis*) and frogs (*Rana pipiens*), but the best bait undoubtedly is "nightcrawlers" (*Lumbricus terrestris*). They spawn on gravel bars, clearing out a depression 2 or 3 inches deep in which the eggs are laid and over which the fish lies, gently fanning the water to keep it in circulation. Any intruder is met by a furious rush and either driven off or devoured. The young bass frequent the shallow water along the edges of the lake, and are not at all confined to the presence of weeds. In fact, in La Belle lake they are most abundant in water a foot deep without a sign of vegetation. The young grow rapidly and reach a length of about 3 inches by fall. Spawning occurs in May, but is hurried or delayed by the temperature of the water, 65° to 68°F being the critical temperatures in Waukesha county. The average size is 2½ pounds, but I have taken specimens 5 to 5½ pounds, these being about the maximum size attained. An excellent table fish, second to none.

72. *Micropterus salmoides* (Lacepede). Large-mouth Black Bass; Green Bass; Oswego Bass.

By far the most abundant of the bass, inhabiting all of the lakes and rivers. While the species is dependent upon bars for breeding purposes, they are not particular, and any ledge two feet wide will do for the purpose. This at once extends the possible distribution of the species over that of the preceding. The green bass is also a fish of the deep water just off of the bars, but those bars must be bordered by weed beds, usually Potamogeton. In these weeds the fish lie, and into these weeds goes the fish with any bait as quickly as possible. The average size is between 2 and 2½ pounds, though bass weighing 5 pounds and over are on rare occasions caught. The largest of which I personally have a record which I know to be authentic is 8¼ pounds, caught in Eagle lake. Between this enormous fish and bass weighing 6 pounds I have no record. The fish breed in May and if the season be backward are often still upon the beds by June 20 when the fishing season opens. These beds are shallow depressions well up on the bars and, if the spawning space be limited, the nests are often as close together as it is possible to put them. Over these beds the male

lies, keeping the water in circulation and sediment in motion until the eggs hatch. Thereafter the male accompanies the swarm of tiny bass for a period of about two to three weeks, protecting them against the ravages of larger fish. The food of the young fish is almost exclusively entomostraca, but they begin their piscivorous habits when about an inch long, eating young shore minnows, darters, etc. The adults are almost exclusively fish-eaters, crayfish playing only a very minor rôle in their diet. Unlike the red-eye, the green bass is active all winter and hundreds are caught through the ice on most of the larger lakes. At this time of the year they inhabit water 10 feet or less in depth and are associated with the silverbass (*Pomoxis sparoides*) which are caught in the same holes. The greenbass bites best on chubs (*H. kentuckiensis* and *S. atromaculatus*) but will also take frogs, crayfish or angleworms. An excellent table fish, prized next to the red-eye.

73. *Scardinius erythrophthalmus* (Linn.). European Rudd; Pearl Roach.

In 1916, Mr. B. O. Webster, at that time superintendent of hatcheries, now a member of the Wisconsin state conservation commission, went to New York at the request of Mr. Fred Pabst of Oconomowoc, and obtained from the New York Aquarium "several pails" of this species. These fish were successfully brought back to Waukesha county and were planted in Oconomowoc lake, where they are doing very well. At present there are three sizes of fish in this lake, indicating two successful spawnings at least. The fish have never traveled more than half a mile from the site of the original planting, at the southeast end of the lake. Knowing the location of the school in a general way, I have caught three specimens since 1918, always on worms as bait. The food of these has been entomostraca, together with insect larvae and small minnows, with a few snails (*Physa*) and small clams (*Pisidium*).

Family PERCIDAE

74. *Stizostedion vitreum* (Mitchill). Wall-eyed Pike.

An introduced species which has been abundantly planted in Golden, Oconomowoc, La Belle, Forest, both Nashotahs and Nemahbins, Laura, Pine, Pewaukee and Nagawicka lakes. Except during the spawning season when they ascend the rivers, the pike is distinctly a lake fish within the limits of the county, but in Rock river just over the boundary it is very abundant. It inhabits the deep water off the bars, ordinarily in the vicinity of weed beds. The fish are of a wandering disposition, here today and there tomorrow, so that their capture is often rather difficult. They spawn early in the spring, ascending the rivers for the purpose soon after the ice goes out. In this respect they resemble the pickerel (*E. lucius*) which they follow and are themselves followed by the various species of suckers. The young wall-eyes return to the lakes rapidly after hatching



and go into deep water where many must fall prey to larger fish. However, young pike are extremely pugnacious and begin their piscivorous diet when 5 or 6 days old. In my collection I have a string of seven wall-eyes of this age, each member of the string with the posterior half of the preceding pike well down his throat. Thus the whole string died. The fish attain a good size; I have records of many weighing between 7 and 10 pounds, and I have no doubt that 15 pounders are not unknown to Golden, Oconomowoc and the Nashotahs. They are frequently the host to the peculiar ectoparasite *Argulus stizostethi* which crawl over them much in the manner of lice.

75. *Stizostedion canadense griseum* (DeKay). Gray-Pike; Sand Pike; Wall-eye.

This species, like the preceding, has been widely introduced throughout the county, and is never distinguished by local fishermen who take it for small fish of the preceding species. They differ from the preceding markedly both in coloration and in size. This fish is distinctly of a gray tinge while the other is very golden. Furthermore, this species is much smaller, seldom exceeding a pound or a pound and a half. They are very abundant in Forest and La Belle lakes, much less so in all the other lakes. Their general habits and food are so nearly like those of the preceding species that they need not be discussed. Decidedly a less desirable table fish because of its smaller size.

76. *Perca flavescens* (Mitchill). Perch.

Abundant in all of the lakes and rivers in the county. The large perch are distinctly a deep water fish, inhabiting the Potamogeton beds in the deep water off the edge of the bars. If one were to make a survey of the water between here and the shore, one would find a gradual decrease in size of the perch correlated with a decrease in the depth of the water, with the young-of-the-year in the very shallow water along the shore associated with *Notropis blennioides* and *N. hudsonius*. The nest is a shallow depression in the sand along the shore and here a string of very beautiful eggs is laid. The young remain in the shallows and attain a length of about three inches by fall. The food of the young is largely entomostraca and insect larvae while that of the big adults is largely crayfish and minnows. Like the green bass (*M. salmoides*) and silverbass (*P. sparoides*) the perch is active and feeding all winter and thousands of them are caught through the ice when they are so heavy with spawn that they can barely flop. Such fish often weigh a pound or a pound and a half. A very excellent table fish, readily caught on either worm or small minnows.

#### Subfamily ETHEOSTOMINAE

77. *Percina caprodes* (Raf.). Log-perch.

A common species of darter in the deeper portions of the larger rivers,

particularly in the Fox and Oconomowoc. It is an inhabitant of water of moderate current and reasonable clearness, avoiding foul or muddy water. The fish prefer a rocky or heavy gravel bottom to sandy bottom, and avoid entirely mud or silt. Very fast in action, they are easily approached but disappear under rocks or stumps as if by magic if disturbed. In this characteristic only do they resemble the other darters. They feed on bottom animal matter almost exclusively, Chironomus, Simulium, Allorchestes and other small crustacea, with occasionally a minute mollusk. They have no particular economic value and are never used as bait because of their small and tender mouth. I have found them as food in *Micropterus salmoides*, *Esox lucius* and *Stizostedion vitreum*.

78. *Hadropterus aspro* (Cope & Jordan). Black-sided Darter.

A darter of the river systems only, taken in all but the Menomonee river, particularly common in the Mukwonago and Fox rivers. A fish of medium current, but preferring water a bit faster than the preceding. Usually found where some vegetation is present into which the fish retreat. Fine gravel is the preferred type of bottom but they are occasionally found over muck, in which case the fish are decidedly darker in coloration. In the Fox river they are associated with *Esox americanus*, *Umbra limi* and *Cottus* sp.; in the Mukwonago especially with *Semotilus atromaculatus*. The food is largely entomostraca and crustacea (copepods) with large numbers of insect larvae and nymphs. Spawning occurs early in June, in shallow water, often under overhanging banks or amid vegetation, in water of some current.

79. *Diplesion blennioides* (Raf.). Green-sided Darter.

Distinctly a stream species, though I have taken the species a number of times in both Oconomowoc and La Belle lakes. Common wherever found, this beautiful little darter prefers a sandy bottom and medium current, being absent from rock and mud environments. On this sand they lie supported by their very ample pectoral fins, as if they were resting on their elbows, ready for instant departure. When they start off, the quick flip of the tail stirs up the soft bottom in a whirl of sand and by the time this settles, the darter is nowhere to be seen, having made good its escape behind the "smoke screen." While I have never seen the nest in a river habitat, I have found several in Oconomowoc lake. These have invariably been under small pieces of water-logged wood, from beneath which protrudes the peculiarly shaped head of the watching fish. This is the male; and if an intruder of considerable size appears, he retreats under his shelter without delay. If the enemy be a small minnow, the male makes a furious dart out of his hole, flies at the intruder, and returns again so quickly that about all one sees is a cloud of sand which conceals for a moment the opening to the nest into which the male has dived. By

the time the sand settles again, the head of the male is once more poking out of the nest entrance. Food is entirely bottom fauna of small size, as entomostraca, small crustacea like *Hyalella* and *Gammarus*, and small mayfly and damselfly nymphs.

80. *Boleosoma nigrum* (Raf.). Johnny Darter.

The characteristic and most abundant darter of the region, found in every lake and in every river and stream. It is equally at home in the swift current of the Bark river and the still waters of the large lakes, its one demand being gravel bottom or coarse sand. Mud it strictly avoids. It is distinctly a shallow water darter, found resting upon the bottom supported by the pectoral fins in true darter attitude. It is not particularly timid, often joining *Notropis blennius* in investigating one's toes when one goes swimming. However, when frightened, Johnny is off amid a swirl of sand and is found in a rigid, expectant attitude when the cloud settles. The eggs are laid on clear sand, no nest being constructed that is worthy of the name, during May and very early June. The food of the species is composed of *Chironomus* and *Simulium* larvae to about 50%; with crustacea (*Hyalella*) and entomostraca (*Cyclops*, *Daphnia*, etc.) composing the other half.

81. *Ammocrypta pellucida* (Baird). Sand Darter.

This peculiar darter is recorded from a single specimen taken by me in the Ashippun river. The region from which it came is one of clear sand over a stretch of perhaps 300 yards, with not a sign of aquatic vegetation of any sort, or of a pebble larger than a sand grain. In looking over this barren stretch I found this darter buried in the sand, with nothing visible but the eyes and mouth. Such is the normal habit of the species: avoiding vegetation they protect themselves by imbedding the body in the soft sand. I know nothing about its breeding habits or its food, as careful search here and in other similar localities has revealed no further specimens.

82. *Etheostoma iowae* (Jordan & Meek). Iowa Darter.

A common species in certain lakes, Oconomowoc, Pine, and La Belle, where it inhabits the shore waters above a sand or fine gravel bottom with some low, submerged vegetation present. Here it is associated with *Boleosoma nigrum*, *Etheostoma coeruleum*, and *Notropis blennius*. While the pectoral fins are well developed, the species has rather less of the darter habit of resting upon them, the fish being more constantly in motion than the Johnny darter. While capable of very rapid motion, the Iowa darter tends to be more deliberate than many other species of darters, though the fish is, of course, a member of the bottom fauna. The food is largely copepods, with some insect larvae and many small mayfly and stonefly nymphs. I have taken gravid females during May and early June.



83. *Etheostoma jessiae* (Jordan & Brayton).

Not an uncommon species in lakes of certain kinds. I took the species first in Oconomowoc lake, but it is much rarer in the large, gravel bottom lakes than in the smaller, soft bottomed lakes and ponds. I have the species from Laura lake, the larger of the Skidmore ponds, Okauchee ponds, Forest lake, and the Genesee lakes. It is a small, inconspicuous darter, rapid in movements, and using the darter trick of stirring up the bottom by a violent flick of the tail in order to hide or escape enemies. It is distinctly a solitary fish, being much less gregarious than any of the preceding species, and seldom more than a single specimen in taken in the net at one sweep. The fish breed in May, but I have taken gravid females in Oconomowoc lake as late as June 12. They spawn in the shallow water along the shore, usually in a clump of submerged vegetation. The food is typical of the darters, being largely entomostraca and insect larvae, mostly Chironomus, but with some nymphs or small crustacea (Hyaella) as well. The species is often rather heavily infected with the cysts of the parasite (?) *Diplostomulum cuticola*.

84. *Etheostoma coeruleum* Storer. Rainbow Darter.

While this species somewhat resembles the preceding, it is a fish of the larger gravel lakes, Oconomowoc, Pine, La Belle, Okauchee, North, Keesus, Pewaukee, Silver, Golden and Beaver. It is in all respects a very typical darter, and one of the most common species of the group. It inhabits the shore water along with *Boleosoma nigrum* and *Notropis blennioides*, and few collections along the lake shores fail to yield two or three of this species. It is very fast in its actions, and resembles *Diplesion blennioides* in its habit of seeking refuge under stones or sticks though it does not remain under objects for any length of time. The fish spawn in May, usually the latter half, laying in shallow depressions well up toward the shore, within the zone of wave action. The food is mostly cladocera and copepods, while crustacea (Hyaella and Gammarus) form about 25% of the total bulk. Often used as bait for silverbass and perch, though not desirable because of the dark color and not very great vitality.

85. *Etheostoma flabellare lineolatum* (Agassiz). Fan-tailed darter.

In delicacy of markings, if not in color, this is one of the most attractive of our darters. It is an inhabitant of very rapid water, being associated most frequently with *Cottus bairdii bairdii* and *Noturus flavus*. It is very local in its distribution, being confined to those parts of the various rivers in which the current is great and the bottom hard. The Little Oconomowoc, Oconomowoc, Scuppernong and Bark rivers contain large numbers of fan-tails where these conditions prevail, and it is a rare fish in the Mukwonago river. They attain a length of 3 inches in the Scuppernong, though the average size is  $2\frac{1}{2}$  inches. The fan-tail is very rapid in its movements, probably the fastest of all the darters, and this speed stands it in good

stead in its habitat. The food is largely insect larvae, *Simulium* predominating when the form is in season. These, together with mayfly and small dragon fly nymphs, *Planaria*, and occasionally young leeches make up the bulk of the food, while entomostraca and tiny gastropods are also items. During the breeding season the cheeks of the male swell up, each spine of the first dorsal fin develops a tiny white mushroom-shaped tip, the color deepens, and the fish becomes really an exquisite example of the darter group. They spawn just below the rapids, usually behind a stone, clearing out a shallow depression in the immediate vicinity of which the now very pugnacious male patrols. Infection with cysts of (?) *Diplostomulum cuticola* is not infrequent, but never heavy. They spawn in June.

86. *Boleichthys fusiformis* (Girard). Spindle-shaped Darter.

This is one of the rarer species of darters in the county, and has been taken by me in Oconomowoc, Pine, and La Belle lakes, and in the Bark river. It is a fish of quiet water and hard bottom, avoiding dirty conditions entirely. A depth of about 18 inches of water is preferred, and the fish show little of the typical darter characters of behavior, rather resembling *Etheostoma iowae* in this respect. I have, however, taken them in tributaries of the Bark river in much shallower water, amid heavy vegetation. Gravid females have been taken in May and only once as late as May 30.

87. *Microperca punctulata* (Putnam). Least Darter.

This tiny darter, by far the smallest of the group, is quite rare in Waukesha county, having been taken by me only in the Bark river north of Rome, on the very western edge of the county. Here, however, it is locally common, inhabiting water of 2 feet or more in depth, heavily loaded with *Potamogeton* and *Elodea*. It avoids any considerable current, preferring the quiet, deep pockets along the muddy shores, associated with young *Pomoxis sparoides* and *Micropterus salmoides*, which in turn feed to some extent on it. Giants of the species measure  $1\frac{3}{4}$  inches, but the average size is under one inch. Their food is entirely animal matter, being about equally divided between insect larvae, nymphs and entomostraca. It is an exquisite little fish whose reticulate markings remind one of the fan-tailed darter (*Etheostoma flabellare lineolatum*) while the lateral markings resemble those of the Johnny darter (*B. nigrum*).

Family SERRANIDAE

88. *Roccus chrysops* (Raf.). White Bass; Striped Bass.

Another introduced species which has taken firm hold in a large number of lakes. In La Belle and Pewaukee the fish are very abundant, while the species is present in somewhat lesser numbers in Oconomowoc and Naga-wicka. The most gregarious of our fresh water fishes, the adult white bass seem at all times to travel in large schools of several hundred individuals while the young are apparently solitary. During most of the year the fish

inhabit the deep water off the sand bars where they can be caught on small shore minnows by deep trolling. However, on quiet hot days in July and August the great schools often come to the surface, frittering along half out of water as they travel rapidly in a zig-zag course. At such times they offer great sport to the dry fly fishermen, as the fish often strike furiously and follow it up with a very game fight in the deep water. They attain a size of over three pounds, with 2 pounds as a good average. Spawning occurs about the middle or end of May, and the fish ascend the rivers if possible, to lay their eggs among the rocks and under the falls or amid the riffles. The ascent of the rivers is usually at night and the spawning occurs at night, as I have often witnessed in the Oconomowoc river below the falls marking the outlet of Fowler lake into Lac La Belle. Here the water is literally alive with white bass for three or four days and nights. As soon as the eggs are laid the fish return to the deep water of the lake. The young remain in the shallows along the banks of the river or return to the lake and follow the shallows of the shoreline where they are taken in association with *Notropis blennius* and young-of-year of *Ambloplites rupestris* and *Lepomis pallidus*. The food is almost entirely small minnows, with occasional insect larvae or nymphs. This food is taken while the fish are in deep water, as stomachs of fish caught frittering along the surface are invariably empty. An excellent game and food fish, the continued planting of which is earnestly urged.

#### Family SCIAENIDAE

##### 89. *Aplodinotus grunniens* (Raf). Sheepshead; Drum.

This species is included in the list solely upon the authority of Dr. I. A. Lapham, who lists it as an inhabitant of Oconomowoc lake in the only published list of fishes of the region (1882). The sheepshead is no longer a native fish in the county, though occasionally young individuals are planted along with shipments of bass, whitebass, perch and catfish from the Mississippi river overflows. Several fingerlings went into Oconomowoc lake in August, 1925. The prevalent idea of the undesirability of the sheepshead as a food fish is not concurred in by the writer, who considers it equal to the white bass and the croppies, and better than the sunfish, pickerel and buffalo.

#### Family COTTIDAE

##### 90. *Cottus bairdii bairdii* (Girard). Sculpin; Miller's thumb.

This peculiar looking fish is a common inhabitant of rapid water regions of the Oconomowoc, Little Oconomowoc, Bark and Fox rivers. It lives only in regions of the greatest current, frequenting the rocks below falls and the riffles of the many small rapids. Here the sculpin is associated with *Noturus flavus* and *Schilbeodes* sps. The great pectoral fins are used in darter fashion to support the body against the current, head upstream.



The movements are likewise darter-like in their rapidity. The fish lie on the bed of the stream or under the edges of rocks, the belly pressed in close contact with the bottom. The food is composed of entomostraca and small crustacea, with occasional insects, stonefly larvae and small dragonfly and mayfly nymphs, Chironomus and Simulium larvae, and rarely a small mollusk.

TABLE 4

A LIST OF THE FISHES OF WAUKESHA COUNTY, SHOWING THE  
NUMBER OF LAKES IN WHICH EACH SPECIES IS FOUND,  
AND THE NUMBER OF COLLECTIONS IN THE  
RIVER SYSTEMS IN WHICH EACH  
SPECIES HAS APPEARED

	Rivers						
	Lakes	Ashippun	Oconomowoc	Bark	Fox	Menomonee	Scuppernon
<i>Lepidosteus osseus</i>	26	9	46	27	14	12	—
<i>Amiatus calvus</i>	31	12	31	28	11	13	16
<i>Leucichthys artedi</i>	13	—	—	—	—	—	—
<i>Salmo irideus</i>	3	1	—	—	—	—	37
<i>Salvelinus fontinalis</i>	1	6	—	9	—	—	82
<i>Salmo fario</i>	3	—	—	—	—	—	47
<i>Anguilla rostrata</i>	2	—	1	—	—	—	—
<i>Ictiobus cyprinella</i>	2	9	12	14	8	—	22
<i>Ictiobus urus</i>	—	7	20	11	9	—	16
<i>Ictiobus bubalus</i>	4	14	17	9	12	1	18
<i>Catastomus commersonii</i>	11	91	37	29	52	31	88
<i>Catastomus nigricans</i>	—	33	16	87	35	16	26
<i>Moxostoma aureolum</i>	10	12	31	62	27	3	11
<i>Moxostoma breviceps</i>	—	1	14	15	6	8	12
<i>Cyprinus carpio</i>	11	34	43	46	72	—	62
<i>Campostoma anomalum</i>	14	63	66	34	41	62	84
<i>Chrosomus erythrogaster</i>	—	a	13	23	—	—	7
<i>Pimephales notatus</i>	38	a	a	a	18	a	a
<i>Semotilus atromaculatus</i>	2	a	a	a	a	8	a
<i>Notemigonus crysoleucas</i>	3	2	—	—	—	—	—
<i>Notropis blennius</i>	41	37	46	39	13	—	35
<i>Notropis whipplii</i>	2	19	27	22	26	—	7
<i>Notropis cornutus</i>	4	a	a	a	a	13	a
<i>Ameiurus natalis</i>	9	22	13	27	17	3	19
<i>Ameiurus melas</i>	21	42	19	36	32	9	25
<i>Leptops olivaris</i>	—	—	—	—	1	—	—
<i>Umbra limi</i>	18	9	2	4	10	—	5
<i>Esox lucius</i>	38	11	52	24	19	—	18
<i>Fundulus diaphanus menona</i>	41	10	13	9	22	16	19
<i>Fundulus notatus</i>	7	1	—	3	—	4	8
<i>Eucalia inconstans</i>	—	—	—	—	—	1	6
<i>Labidesthes sicculus</i>	28	19	26	20	11	2	9

(Continued)

Species	Rivers						
	Lakes	Ashippun	Oconomowoc	Bark	Fox	Menomonee	Scuppernon
<i>Pomoxis sparoides</i>	13	1	6	—	—	—	—
<i>Amplolites rupestris</i>	36	a	a	a	a	4	a
<i>Lepomis cyanellus</i>	27	25	49	23	31	8	21
<i>Lepomis incisor</i>	41	68	71	44	37	14	68
<i>Eupomotis gibbosus</i>	40	19	63	31	25	3	22
<i>Micropterus salmoides</i>	37	45	87	72	a	17	31
<i>Micropterus dolomieu</i>	17	9	2	33	17	—	—
<i>Stizostedion vitreum</i>	19	—	3	—	8	—	—
<i>Perca flavescens</i>	41	52	a	47	63	10	26
<i>Percina caprodes</i>	9	14	8	3	11	1	—
<i>Boleosoma nigrum</i>	35	57	a	a	29	33	18
<i>Etheostoma iowae</i>	21	5	19	5	1	3	8
<i>Etheostoma coeruleum</i>	8	12	17	9	16	3	11
<i>Etheostoma flabellare</i>	3	19	22	10	8	31	18
<i>Roccus chrysops</i>	9	—	—	—	—	—	—
<i>Cottus ictalops</i>	—	2	21	13	—	—	—
<i>Ictalurus furcatus</i>	2	—	—	—	—	—	—
<i>Cristovomer namycush*</i>	3	—	—	—	—	—	—
<i>Coregonus albus**</i>	2	—	—	—	—	—	—
<i>Salmo sebago***</i>	2	—	—	—	—	—	—
<i>Oncorhynchus tshawytscha°</i>	1	—	—	—	—	—	—
<i>Esox masquinongy°°</i>	—	—	—	—	2	—	—
<i>Etheostoma jessiae</i>	7	2	4	1	1	—	2
<i>Hybopsis kentuckiensis</i>	1	a	a	a	44	23	36
<i>Cliola vigilax</i>	—	19	7	—	12	2	7
<i>Esox vermiculatus</i>	—	—	—	—	10	—	—
<i>Hadropterus aspero</i>	4	5	2	18	3	11	4
<i>Lepomis euryorus</i>	—	1	—	—	—	1	—
<i>Lepomis humilis</i>	—	1	1	—	1	—	—
<i>Opsopoeodus emiliae</i>	2	3	3	—	—	—	2
<i>Ameiurus nebulosus</i>	10	4	19	13	3	1	14
<i>Pomoxis annularis</i>	5	—	—	—	1	—	—
<i>Aplodinotus grunniens</i>	—	—	1	1	—	—	—
<i>Fundulus dispar</i>	3	—	—	2	4	1	—
<i>Notropis atherinoides</i>	—	3	1	1	4	—	—
<i>Stizostedion canad. griseum</i>	8	—	—	—	—	—	—
<i>Schilbeodes exilis</i>	—	12	8	2	6	1	3
<i>Hybognathus nubilata</i>	—	—	1	—	—	—	—
<i>Diplession blennioides</i>	2	1	5	1	4	2	—
<i>Notropis hudsonius</i>	21	42	18	14	10	19	23
<i>Microperca punctulata</i>	4	—	—	—	—	—	—
<i>Etheostoma zonale</i>	5	1	9	13	1	—	8
—	—	—	—	—	—	—	—
Number of species:	48	55	53	49	51	37	46

- \* 690,000 planted 1877, 1878, Oconomowoc and Nagawicka lakes; no sign of the species now.  
 \*\* 350,000 planted 1887 in Oconomowoc lake; probably gone.  
 \*\*\* 12,000 planted 1879 in Oconomowoc and Nagawicka lakes; gone.  
 0 6,300 planted in Oconomowoc lake in 1879; gone.  
 00 Formerly in several of the rivers; now exterminated.

TABLE 5  
 Total Planting of Fish in Waukesha County, From 1877 to 1918\*  
 (Compiled from records of the State Game Commission)

Year	Brook Trout	Rain-bow Trout	Wall-eyed Pike	Carp	Black Bass Fry	Black Bass Fingerling	White Bass	Perch	White-fish	Lake Trout	California Salmon	Land-Locked Salmon
1877	10000									360000 330000	(1) 4800 — (2) 1500	12000 (2)
1878	—											
1879	—											
1880	—											
1881	20000											
1882	20000											
1883	10000											
1884	20000	20000	1300000									
1885	15000	—	2650000									
1886	55000	—	850000	135								
1887	50000	30000	1100000	250					350000 (1)			
1888	85000	—	800000	975								
1889	90000	85000	1200000	75			2500					
1890	80000	165000	2080000	200			—					
1891	80000	80000	1800000	800			—					
1892	50000	80000	300000	750			—					
1893	25000	10000	800000	100	14000		—					
1894	40000	—	1500000	50	9000		1700					
1895	16000	—	3400000		27500		—					
1896	25000	40000	1500000		35600		5050					
1897	14000	6000	1800000		—		3525					
1898	33000	40000	2850000		15200		7800					
1899	20000	—	2660000		15900		2500					
1900	33000	40000	8960000		—		—					
1901	18000	25000	1800000		—		—					
1902	40000	22000	2000000		3600		—					
1903	24000	30000	1740000		45000		—					
1904	—	—	100000		44000	10300	—					
1905	15000	6000	6850000		30000	1800	5950					
1906	17500	7500	5480000		127000	—	—					
1907	20000	15000	2400000		50000	—	—					
1908	42000	27000	9100000		4000	44300	—					
1909	28500	20400	11800000		27700	46000	—					
1900	30000	46500	3720000		96000	12300	—					
1911	40000	32000	22020000		47500	14275	—					
1912	103000	22000	16900000		6000	—	—					
1913	76000	27000	11670000		12000	111925	—					
1914	93000	51000	8795000		—	102000	—					
1915	95400	39200	6672000		—	91000	—					
1916	56000	26400	7192000		—	4847	3840 4440					
1917	48000	44200	5690000		115500	—	4200					
1918	42000	57800	8950000		122500	—	—					
Total:	1579400	1095000	165429000	3335	848000	438747	29025	12480	350000	690000	6300	12000

(1) Oconomowoc Lake. (2) Nagawicka Lake.

\* No accurate data are available since 1918.



TABLE 6  
 Plantings of Pike, Black Bass and White Bass in Certain  
 Lakes, Between 1895 and 1908 inclusive\*

Lake	Wall-eyed Pike	Black Bass	White Bass
Oconomowoc	2,900,000	43,600	3,850
Pewaukee	5,140,000	68,950	1,000
Okauchee	5,065,000	59,200	4,900
La Belle	3,200,000	30,100	4,050
Pine	2,175,000	11,500	2,625
Nemahbin	2,720,000	26,400	1,500
Nagawicka	4,735,000	26,100	2,250
Silver	1,850,000	4,600	200
Nashotah	3,650,000	8,500	1,600
Keesus	920,000	9,000	—
Beaver	1,900,000	28,100	700
Moose	1,550,000	35,100	—
North	60,000	—	—
Ashippun	1,050,000	3,000	—
Lake Five	1,430,000	—	—
Eagle	2,210,000	7,750	—
Forest	200,000	4,500	900
Crooked	150,000	7,000	500
Fowler	2,250,000	4,500	500
Hunter	180,000	27,000	—
Golden	—	20,000	500

\* No tabulated data available since 1908.

THE BROOK SILVERSIDES *LABIDESTHES SICCULUS* (COPE)

## INTRODUCTION AND DESCRIPTION

The brook silversides, *Labidesthes sicculus* (Cope), which in southern Wisconsin is characteristically not a brook species at all, being found most commonly in clear water lakes, is one of the most abundant and typical species of lake minnows found in Waukesha county. While its abundance varies considerably in the different lakes, yet it has been found in all of the lakes of considerable size (28 in number, table 4) and is conspicuously absent from the small, muddy-bottomed ponds, and from all lakes and rivers whatsoever their size in which the water is not clear.

This little species is the only Wisconsin representative of the family Atherinidae of Linnaeus (1758). These fish, known generally as the "friars" or "silversides" compose a family whose members are typically salt water forms. The family is composed of sixteen genera and about seventy species, none of which attains a large size. Among the more familiar genera can be listed *Atherina*, the friars; *Chirostoma* Swainson; *Menidia* (Bonaparte) Jordan and Gilbert; *Atherinopsis* Girard; *Atherinopus* Steindachner; and *Labidesthes* Cope. Of these genera, *Menidia* is the closest to *Labidesthes* both in morphological characters and in general habits, as *Menidia*, typically a marine genus, often ascends streams and rivers, passing from the brackish water environment to the fresh water conditions beyond the tidal zone. Structurally *Labidesthes* differs from *Menidia* in the prolongation and depression of both jaws to form a "beak" which characteristic gives the name to the genus—"a pair of forceps." The name is well chosen, and gives a clear picture of the daintiness of the mouth structure. The Atherinidae are all carnivorous in their habits and in common all the species have a straight gut lacking entirely pyloric ceca. The small size of the individuals makes them of little economic importance as food fishes but those which reach a size sufficiently large to warrant attention are highly valued as food, hence the common name of some of the marine species: "Pez del Rey"—fishes of the king! This applies particularly to the genus *Menidia*, and more especially to *Menidia sardina*.

The genus *Labidesthes* was created by Cope in 1870 to hold the type species, *sicculum*, originally described by himself as *Chirostoma sicculum* in 1865, the type specimen coming from the region of Grosse Isle in the Detroit river. This places the type locality as the inlet of the Detroit river into Lake Erie, some twelve miles south of Detroit, Michigan. The genus comprises a single species, of which the following description is given by

Jordan and Evermann (1896: 805): "Head  $4\frac{1}{2}$ ; depth 6; eye  $3\frac{1}{2}$ ; D. IV-1, 11; A. 1,23; scales 75. Body elongate, very slender, compressed. Head long, flattened above, narrow below. Snout slender, conic. Premaxillaries broad posteriorly, very protractile, produced forward, the snout longer than the eye. Edge of upper jaw strongly concaved. Teeth very slender, mostly in one series, forming a narrow band in front. Scales small, thin, with edges entire (cycloid). Spinous dorsal very small; soft dorsal short. Anal fin long, caudal forked; pectorals moderate. First dorsal inserted somewhat behind the vent. Pale olive green, translucent; lateral silvery band very distinct, scarcely broader than pupil, bounded above by a dark line; back dotted with black. In the black waters of the lowland swamps the silvery is underlaid by black. Length  $3\frac{1}{2}$  inches. Ponds and sluggish streams; Lake Ontario and southern Michigan to Iowa, Florida and Texas; locally abundant; a very graceful little fish, widely distributed, confined to fresh waters." The present writer can offer no improvement on the above description beyond pointing out the fact that the tendency of the black pigment to underlie the silvery band is evident in a vast majority of the specimens from southern Wisconsin where the water is anything but like the "black waters of the lowland swamps."

In spite of the familiarity of all ichthyologists with this attractive species, and despite the fact that it is listed as common or abundant in practically every list of fishes of the Mississippi valley, no comprehensive study of the species has been published, nor are observations of the habits or general behavior of the species to be found in other than the most general terms. "Beyond observations that *Labidesthes* remains near and feeds at the surface and that it frequently skips through the air, nothing has been published concerning the habits of this fish" (Hubbs 1921). Notes on its food have been presented by Forbes (1878, 1883, 1888), Forbes and Richardson (1908), Baker (1916, 1918), Evermann and Clark (1920), Pearse (1915) and Hubbs (1921). This represents the status of our knowledge at the time of publication by Hubbs (1921) of his ecological study of the life-history of the species in 1921. This report contributed considerable to our knowledge of the species and pointed out several problems which enter into the life-cycle of the fish from a behavioristic standpoint. Explanations of these problems are offered, but they are essentially theoretical in nature, and the present writer, as a result of five years of observations and as a result of experimental procedure, finds it necessary to disagree with Hubbs in some of his conclusions. Several important points in the behavior of the species have been entirely overlooked by the previous author, and several errors appear as a result no doubt of having failed to find these facts. Thus he says: "In striking contrast to their intense activity by day, the adults at night were observed to lie quiescent as though asleep." This statement points to entirely erroneous conclusions,



for under certain conditions, and at certain times of the year the "intense activity" of the species during the day is as naught compared to the frenzied activity of the species *at night*. A small point, perhaps, but the key to many of the problems requiring solution in a study of the life history of the silversides.

#### BREEDING HABITS

The adult of *Labidesthes sicculus* is primarily a shallow water inhabitant. After the fish has attained approximately two thirds of its mature size, the species takes up permanently a shallow water habitat which is in direct variance with the habits of the immature fish. Both young and adults are surface species, living normally within less than a meter of the surface of the water, and spending most of their time within ten or twelve centimeters of the surface. Indeed, the species is the most consistently "top-water" fish in these fresh water lakes, distinctly more so even than the gar, *Lepisosteus osseus*. The gar often seeks very deep water when it feeds, grasping a minnow sideways the fish descends at an angle of about 45° to a depth of from ten to thirty feet, where the juggling which accompanies the adjustment of the food into a position permitting its entrance into the small mouth takes place. After feeding the gar may remain in the deep water for some time, upward of fifteen minutes, before ascending slowly to the surface. The silversides never under any conditions descends below the upper meter of water, this being the maximum depth sought by the adults, while nothing can drive the immature individuals more than a few centimeters below the surface. Hence the statement that the silversides is the most characteristic of our surface fishes. It is as typical of the upper stratum of water as the Johnny darter (*Boleosoma nigrum*) or Miller's Thumb (*Cottus bairdii bairdii*) is of the very bottom of the lakes and rivers.

The breeding habits occur during May and June under normal, seasonable conditions, the exact time being closely correlated with the temperature of the water. As the surface waters warm up under the influence of the May sun, the silversides are to be seen swimming near the shores often in pairs. As there is no sexual dimorphism it is impossible to distinguish the sexes while the fish are in their element, but repeated captures and laboratory examinations show that the two individuals associated at this time are male and female. The fishes often swim in perfect alignment, one *above* the other, a distance of approximately ten inches to a foot intervening. This alignment is under the control of the upper fish which, because of the position of the eyes, can keep the lower individual under observation. This was repeatedly borne out by observations which showed the fact that when the path of progression deviated from a straight line, the first sign of the turning was made by the lower fish. The upper fish is the male, the lower the female. Frequently two, three or more males may

be associated with a single female during the height of the spawning season, but this poly-association usually terminates by one of the males driving away the others. During the early part of the breeding season the progress of the fish is leisurely, a foot being traversed in from three to four seconds. As the breeding season advances and the water warms up still more, the speed of progression increases until the fish travel in spurts, covering a foot in a fraction of a second and often breaking water. At the same time the interval of alignment has been decreased to about two inches, and finally, as the breeding season reached its peak, the position is shifted to a *horizontal* one, the male following the female which travels at a furious pace. A school of silversides reveals a wild sight when the spawning activities are in full sway. In and out dart the females, pursued by one or more males, darting this way and that, shooting an inch or more out of the water and landing again three or four inches from the spot of their emergence amid a spatter of spray, followed immediately by the attending male retinue. Suddenly the female slows down her pace and comes to what amounts to *comparative* rest. The first male to reach her approaches from the rear and draws up along side. This apparently is the signal for the departure of any other males that may be pursuing that particular female, for never have I seen any disturbance once a male is associated along side of a female. Other males simply disperse and join in the chase of other females. The paired fish now begin a downward glide, approaching the bottom at an angle of approximately  $30^{\circ}$ . During the descent, the fish bring the edges of their abdomens into repeated momentary contacts—from eight to twenty-one times being the extreme numbers observed, with fourteen as an average of forty-six observations. During the descent the eggs are extruded from the body of the female and may be seen slowly settling toward the bottom in the wake of the descending pair. Fertilization takes place in the water immediately after the eggs leave the female, the spermatozoa being extruded by the male coincident with the momentary contact with the abdomen of the female. By the time the pair reach the bottom the egg complement has been deposited. Observations on twenty-six females captured immediately after the completion of the descent, show the ovaries empty, with only occasionally (three cases) some half dozen eggs still retained. Normally the female is entirely spent on the completion of a single breeding performance, and hereafter she is completely ignored by the still active males. The males, on the other hand, hesitate not at all on the completion of the breeding descent, but ascend at once to the surface and are off in pursuit of other females.

A series of observations over four breeding seasons in which a series of temperature readings of the water was taken during the period of breeding activity, shows that the vertical pairing of the fish begins when the water has reached a temperature of  $18^{\circ}\text{C}$  ( $64.4^{\circ}\text{F}$ ), that the spawning begins at a

temperature of 20°C (68°F), and reaches its climax with the water at a temperature of 22.4°C (72.9°F), the place of observation being the north shore of Oconomowoc lake, where the silversides breed abundantly over the sand and gravel bottom. These facts are brought out in table 7.

TABLE 7  
TEMPERATURE OF WATER OF OCONOMOWOC LAKE ASSOCIATED  
WITH BREEDING PHENOMENA OF *LABIDESTHES SICCULUS*

	Degrees Centigrade				
	1920	1921	1922	1923	Av.
Vertical pairing first noted	18.3	17.8	17.7	18.2	18.0
First spawning noted	20.3	20.0	20.0	19.7	20.0
Climax of spawning	23.2	22.1	22.3	22.1	22.4

After extrusion the egg settles slowly to the bottom. It is armed with an "organ of fixation," consisting of a single gelatinous filament of a length equal approximately to six times the diameter of the egg. This is called by Hubbs an organ of *flotation*, but its primary function seems, rather, to be that of *fixation*. It adheres to the first thing with which it comes in contact, either vegetation or bottom material, and the egg is firmly attached. Where spawning occurs in rivers, the secondary function of flotation may well be of some importance in relation to distribution by current, but as the species is so active and this activity carries it such long distances, this slight distributional value must be regarded as subordinate to the fixation function. As the egg itself is not at all viscous, it would become buried in the debris and sand at the bottom, did it not become fixed before reaching it.

#### DEVELOPMENT

Nothing whatever is known regarding the embryological development of the species, and the present writer has not considered this phase of the life of the species as within the scope of his problem. That development is quite rapid is indicated by the fact that eggs hatched in eight days in the writer's laboratory in water kept at approximately 25°C (77°F). This temperature is two degrees above that of the lake from which the specimens were taken. Observations on eggs located in the lake and observed daily indicate that the hatching period is very close to 8 days (between 8 and 9) with the water at 23°C. That temperature affects the rate of development is very probable from what is known concerning other species, in which the rate of development increases with an increase in the temperature of the water; therefore one would expect a variation in the normal hatching periods of the eggs in a lake depending upon the fortuitous chances of the eggs becoming fixed in water of varying depths. For it must be remembered that since the eggs are laid in shallow water, a considerable range of temperature variation will be encountered, the range being greater the



shallower the water is. One would therefore expect the eggs that drift into shallow water to hatch earlier than those that settle in deeper water, as they receive more degree-hours of heat per day. Such conclusions are borne out by the facts as shown in table 8.

TABLE 8  
EFFECT OF DEPTH OF WATER UPON THE HATCHING  
PERIOD OF EGGS OF *LABIDESTHES SICCOLUS*

Depth of water: inches	Eggs laid	Eggs hatched	Average noon temp.	Time required
16	6/14/23	6/22/23	24	8
22	6/14/23	6/23/23	23	9
29	6/14/23	6/23/23	23.2	9
37	6/15/24	6/24/24	22.8	9

#### THE YOUNG

Immediately after hatching the young silversides wiggle themselves to the surface. The term "wiggle" is used advisedly as best describing the action of the young fish: the activity consists of much lateral movement with relatively little forward progression. The activity of the fish begins before it leaves the egg, and is responsible for the rupture of the egg membranes and the subsequent liberation of the fish. Once the young reach the surface it is a long time before they see the bottom of the lake again, for they remain permanently just under the surface of the water for the following weeks, and never forsake the upper few centimeters under any circumstances. Their relation to the surface may be stated in these terms: the younger the fish the closer to the surface film of the water do they remain. Newly hatched *Labidesthes* frequent the upper three centimeters or less of their habitat.

As they hatch, then, the young work to the surface, where they congregate in rapidly increasing numbers. Inasmuch as the eggs laid by a single female in the course of her breeding activities do not scatter very far—there is no current in the lake sufficient to cause a wide dispersal—all hatch at very nearly the same time. Thus are built up at the surface schools of young silversides varying in component numbers from thirty to perhaps two hundred. The individual fish are constantly active, swimming around in a course conspicuous for its irregularities. Yet there is a certain co-ordination within the school: if the school is going ahead, all the members are going in a course almost exactly parallel to each other; if the school veers to the right, all the members shift in the same direction and almost at the same instant. While the course of the school is therefore very irregular and the progress in any one direction slow and uncertain because of the many turnings and twistings of the path of progression, the school

is very evidently heading for the deep water, or rather, for the surface water over a pelagic habitat. For be it remembered that of the deep water itself and its contents, *Labidesthes sicculus* knows nothing, nor in its entire existence does it ever learn by exploration what the depths contain.

By the end of the first day the young are well out of the shallows, but unless the deep water be close to the shores—that is, unless the sand bar is narrow—they will still be over relatively shallow water. The one outstanding feature of the behavior of the young during the day is their activity; during three years of intensive observation on the species the writer has *never* seen a living, healthy silversides that was not in action. While I have seen hundreds of thousands of these little fish in dozens of different lakes and streams of every size, I have never during the hours of daylight, seen one at rest for a period of time measurable with a stop-watch. It is by all odds the most active minnow of our fresh waters, and were it not for the fact that this activity is, during most of the year, confined to the hours of daylight, I would venture the statement that it is the most active of all our fresh water species. As it is, this honor must go to the cisco (*Leucichthys artedi*) later to be discussed, which is active day and night the years around. Yet, during the hours when it is active, no fish is more active or vigorous. Certainly no fish covers more distance in the course of the hours of daylight than does this, in relation to its size. Some idea of this activity is brought out in the following experiment: Six young silversides were brought into my laboratory and placed in a large boiler, where they were permitted to swim around and get over any shock their transfer from the lake might have caused. Two hours later, when their activities were perfectly normal, a tracing was made on a large sheet of wrapping paper of their individual movement for a period of two minutes. While watching the movements of an individual fish I traced as nearly as possible its every movement. At the end of the experiment the distance traveled was measured. The results follow.

TABLE 9  
DISTANCE TRAVELLED IN TWO MINUTES BY YOUNG  
*LABIDESTHES SICCULUS*

Fish No.	Length cm.	Distance cm.
1	2.2	176
2	2.4	234
3	2.0	211
4	2.2	220
5	2.1	209
6	2.3	216
Average:	2.2	211

On this basis one can figure as follows: 211 cm in 2 minutes; that is 6,330 cm per hour; and since this is early summer, one can figure at least fourteen hours of activity, which gives 88,622 cm traveled in the course of a day, by a fish that is 2.2 cm long. That is 40,283 times its length!

Throughout the day these tiny, semi-transparent fish work their way incessantly back and forth just under the surface of the water. Their small size, together with their inconspicuous coloring and nearly transparent bodies affords them a protection against wandering enemies, both in the water and in the air. At the approach of a boat the school breaks up immediately, the individuals darting like lightning in every direction except down. When the school is broken up the tiny individual fish is extremely difficult to see, while its zig-zag course makes it difficult to capture even after it is discovered. The approach of a tern (*Clidonias nigra surinamensis* or *Sterna hirundo*) sends the fish scattering wildly, and a similar reaction follows the approach of a larger fish either from below or from their own level. This indicates a keen alacrity on the part of the silversides, which no doubt saves many of them from destruction, for they have many enemies.

With the coming of darkness, however, all this changes. The incessant activity dies down with the failing light until darkness finds the fish entirely inactive, floating motionless just under the surface. Thus they remain throughout the night, drifting back and forth with the waves, or hanging suspended under a glassy surface. Little co-ordination exists within the school at night, for a spotlight flashed upon the school shows the fish pointing in all directions: there is no marked orientation. This is particularly true on quiet nights. When the surface is agitated by wind, however, there is a vague indication of orientation with a tendency on the part of the individuals to head into the waves. The following table (10) shows the results of a series of observations on orientation in relation to the prevailing night wind.

TABLE 10  
ORIENTATION AT NIGHT OF *LABIDESTHES*  
*SICCULUS* IN RELATION TO WIND

Date	No. fish in school	Direction wind	Number of fish heading							
			S	SE	SW	W	E	N	NE	NW
8/6/23	31	S	8	4	5	3	5	0	2	4
8/12/23	49	SE	6	12	9	5	2	5	3	7
8/13/23	26	None	3	5	2	4	3	2	4	3
8/20/23	44	S	12	6	8	4	5	3	2	4
8/25/23	58	S	16	10	4	8	7	4	5	4
8/27/23	36	E	5	5	4	0	11	3	5	3
8/30/23	41	None	3	2	7	6	4	9	6	4
9/12/23	22	N	0	1	0	0	1	12	2	4



It will be noted that in every case the tendency is to orientate to face the waves, but in only one case is even one-half of the school oriented.

As the writer had no instrument for measuring the light intensity, the Eastman Kodak Company's exposure-meter was used as the basis for the determination of the amount of light present when activity ceased in the evening and began again in the morning, and this method proved satisfactory in as far as it goes. The principle involved in this instrument is the exposure of a piece of photographic paper until it darkens to match a color shade on the dial of the instrument. Since one piece of paper may be used twenty times or more by exposing only a small surface of it at a time, the method of comparing light intensities is fairly accurate after one has had a little experience matching colors. As a result of a series of experiments dealing with the intensity of light at which activity ceases at night and begins again in the morning, the writer finds that the light is slightly less intense when activity begins than when it ends. This conclusion is reached from the following data:

TABLE 11  
TIME REQUIRED FOR PHOTOGRAPHIC PAPER TO MATCH DIAL SAMPLE  
COLOR, IN THE MORNING AND EVENING AT THE TIME  
ACTIVITY CEASES AND BEGINS AGAIN

Time in Seconds		
	Morning	Evening
	64	53
	72	70
	56	58
	53	44
	65	50
	62	61
	59	46
	61	54
	55	43
	70	62
	62	60
	88	52
	74	48
	64	46
	67	52
	64	50
	68	44
Average:	65.32	52.59

Since the length of time required to darken the paper is a measure of the light intensity, and since the more light present the shorter will be the time required, one may say that the time required is inversely proportional to the amount of light present. In the case of *Labidesthes sicculus* it appears,

then, that the fish are 23.44% more sensitive to light in the morning than they were in the evening. From this one must conclude that the sensitivity of the fish to light increases in the absence of light, which is perhaps not surprising when one recalls that the fish lives at the very surface of the water where it receives at all times the maximum amount of light. This sensitivity to light following a period of darkness was checked in the laboratory by confining a number of fish in the total darkness of a photographic dark room for varying periods of time. Each fish was kept in a separate dish, and the following data were taken (table 12):

TABLE 12

LIGHT INTENSITY IN TERMS OF SECONDS OF EXPOSURE OF THE EXPOSURE METER, AT WHICH FISH REACT AFTER CONFINEMENT IN DARKNESS FOR VARYING PERIODS OF TIME

Fish number	Number of hours kept in dark			
	34	48	72	96
1	54	47	42	48
2	63	44	39	42
3	58	46	38	40
4	60	48	42	42
5	52	30	33	28
6	50	34	30	32
7	46	30	25	25
8	41	42	40	38
9	49	44	36	36
10	55	46	38	36
Average:	51.8	46.1	36.2	36.7 seconds

In this experiment the light from a 100 watt Mazda light was permitted to fall upon the fish, and the length of time required for their reaction was noted. Thus one finds that up to a certain point, namely 72 hours, the sensitivity to light increases, and that beyond this point there is practically no change. Confinement in total darkness for 48 hours has increased their sensitivity 11% over what it was when confined for 24 hours; that this sensitivity is increased 21.25% when the fish are confined in darkness for 72 hours over that recorded for the 48 hour period, and that the total increase in sensitivity is 30.11% when kept in the dark for 72 hours over that recorded for the 24 hour period. This bears out one of the fundamental principles of physiological ecology: that a factor becomes of increasing importance to an organism when there is the least of it.

#### GROWTH OF THE YOUNG

During the period immediately following the hatching, the young silversides grow rapidly. This growth approximates very closely the surprising total of a millimeter a day for a period of nearly two weeks, this

period being the first two weeks of the life of the minnow. This period of rapid growth gradually passes into one of slower increase, which lasts from about the second week in July through August. A second rapid growth period starts about the first week of September and continues for about three weeks, ending with the cooling of the water late in that month (see figures 11 and 12, which should be considered together). By the end of September the fish have reached a length of 6.5 cm, and this length is not increased during the winter period, as specimens caught in December, February and April show no appreciable increase in length. As the water warms up toward the end of April, however, a new growth stage is inaugurated with the increased activities of the fish, so that the mature size of 7.62 cm is reached at about the spawning season, though data indicate that there is often a slight growth even after the deposition of the eggs. In obtaining data from which these conclusions could be drawn regarding the growth rate of the species two hundred and fifty individuals were measured and the average of the lot was taken as the mean size on the date of capture. Figure 13 shows the number of individual fish of different lengths as taken on August 1, 15, 29, September 12 and 26. Two precautions were taken to unify the results: all adults captured were excluded from the tabulation, and the individuals used for measurements were obtained from as many schools of fish as practicable without too much waste of time in hunting for them, as the schools of very young *Labidesthes* are at times provokingly difficult to locate in a large lake. During the months of ice, the species is rather difficult to capture, as the number of individuals is greatly reduced (the reason for which I shall discuss shortly) the schools are very much broken up and the fish somewhat sluggish in movement. The following table shows the number of fish measured on different dates, together with the average size of the individuals involved. In all cases the measurements were taken from the tip of the snout to the base of the caudal fin.

In this table correction must be made for those variations which have been starred because of the small number of individuals involved. The small numbers are due to the difficulties encountered in securing the fish during the period when the lake is covered with ice. The figures, however, tend to indicate that there is no appreciable increase in size during these months.

It is interesting and important to note that the change in growth rate which occurs toward the end of July, as shown in figure 22, is intimately correlated with two important changes in the habits of the fish: 1) the assumption of a shallow water habitat in place of the deep water situation; and 2) the change from an entomostracan diet to a mixed ration of entomostraca and insects, which is merely a transition stage leading to a culmination in an almost entirely insectivorous diet which is characteristic of the



TABLE 13  
MEASUREMENTS OF *LABIDESTHES SICCOLUS* FROM LAKE  
OCONOMOWOC FROM JUNE, 1922, TO JULY, 1923

Date	No. Fish	Average length in mm	Growth in mm
6/22/22	254	11.2	—
6/29/23	250	20.0	9.8
7/6/22	252	28.6	8.6
7/13/22	255	35.8	7.2
7/20/22	255	39.1	3.3
7/27/22	253	40.2	1.1
8/2/22	250	41.9	1.7
8/17/22	252	46.2	4.3
8/31/22	253	48.8	2.6
9/7/22	250	53.3	4.5
9/14/22	250	58.0	4.7
9/28/22	251	63.9	5.9
10/5/22	250	65.1	1.2
10/12/22	255	65.5	0.4
10/26/22	250	65.6	0.1
1/3/23	10	65.6*	—
2/5/23	8	65.2*	—
3/2/23	21	65.5*	—
4/6/23	35	65.4*	—
4/27/23	15	64.9*	—
5/4/23	112	65.6	—
5/18/23	170	68.6	3.0
6/1/23	185	72.2	3.6
6/8/23	116	73.0	2.2
6/22/23	80	75.2	2.2
7/6/23	110	76.0	0.8
8/1-9/1/23	370	76.2	0.2

\* Numbers too small to be significant.

adult. This point will be discussed in detail under the heading of food habits. The change from the position over deep water to the shallow water habitat will be considered at once.

#### MIGRATION OF THE IMMATURE FISH

I have repeatedly stated that after hatching the young leave the shallow water and travel toward the deep. During the first month or six weeks after hatching the silversides is to be found *only* over the deep waters of Oconomowoc lake and other bodies of water investigated (La Belle, Fowler, Golden, Silver, Upper and Lower Nashotahs and Nemahbins, Okauchee and Pine lakes). Occasionally a school will be located well over the edge of the sand bars in water from three to five meters deep, but far outnumbering these are the schools found over the water of a depth of from 10 to 20 meters. During July, 1923, the writer located 460 schools of silversides in Oconomowoc lake, and measured the depth of the water at

the point where the schools were found. Every effort was made to equalize the search over both shallow and deep water, and an equal length of time was spent hunting for schools in water of the different depths. The results are shown in table 14. Since the edge of the bar occurs in water between 5 and 6 meters deep, a total of 14.77% of the schools occurred upon the bars as against 85.23% over the deep water. The difference is sufficient to show a decided preference on the part of the fish for a pelagic habitat over deep water.

TABLE 14  
THE DISTRIBUTION OF SCHOOLS OF YOUNG LABIDESTHES OVER  
WATER OF DIFFERENT DEPTHS (OCONOMOWOC LAKE) IN JULY, 1923

Depth in meters	Number of schools	Percent of total
0-1	0	0.00
1-2	2	0.43
2-3	14	3.04
3-4	18	3.91
4-5	12	2.61
5-6	22	4.78
6-7	16	3.48
7-8	14	3.04
8-9	31	6.75
9-10	20	4.35
10-11	16	3.48
11-12	44	9.57
12-13	31	6.75
13-14	36	7.83
14-15	32	6.97
15-16	29	6.30
16-17	40	8.70
17-18	16	3.48
18-19	36	7.83
19-10	31	6.75
	460	100.00

However, this distribution of immature fish undergoes a radical change toward the end of July. This fact was discovered quite by accident while investigating a very different problem—the distribution of the shore fish at night as compared to daylight dispersal. Beginning late in June, 1923, the writer collected the fish present along a given strip of shore line on Oconomowoc lake after dark and again at noon over the same area and listed the species found. This area was seventy-five feet in length and was dragged with a twenty foot fine meshed minnow seine. Silversides were found in almost every collection, but more commonly at night than in the day time, and all the specimens were fully grown. It was decidedly interesting, therefore, to find, on the night of July 10, five young silversides in the

collection, these young averaging 1.4 cms in length—evidently early-hatched young of the year. Not one was found in the day seinings. Hereafter, with occasional exceptions, young *Labidesthes* were found every night in the shallow water, and were conspicuously absent during the day from the same region. The one factor which kept the fish from the shallows at night was the condition following occasional heavy rains when the shallow water was in a state of great turbidity. Attention was therefore centered on this migration phenomenon and its progress investigated from various angles. Beginning with July 21, an increase in the number of silversides found each night was noted, and this increase reached its climax on August 6, when the astonishing total of 621 young silversides was collected in a single drawing of the net. Investigation was immediately started at other points along the shore to determine if this was merely a local condition, with the following results:

TABLE 15  
DISTRIBUTION OF YOUNG *LABIDESTHES SICCOLUS* IN OCONOMOWOC  
LAKE ON THE NIGHT OF AUGUST 6 IN RELATION TO TYPE  
OF BOTTOM SELECTED

Type of bottom	Location	No. fish found
Gravel	North shore	621
Sand	South shore	316
Gravel	South shore	508
Rushes on gravel	North shore	141
Potamogeton on gravel	Northeast shore	12

From this table two conclusions can be drawn: 1) that the condition noted was not a local exception but a general rule, that throughout the lake there was a great inshore migration of young silversides; and 2) that these young fish showed a preference to a gravel bottom relatively free from plant growth, that the increasing abundance of vegetation reduced markedly the number of young inhabiting the location. A mechanical error may creep into these figures because of the increasing difficulty of drawing a seine through heavy weeds, but as the silversides is strictly a surface inhabitant, this error is reduced to a minimum as the surface water is covered with reasonable efficiency even in the presence of heavy bottom vegetation. The next morning the same areas were re-seined, with the result that only 38 young were found. Of this number 21 were evidently injured, and probably were cripples left over from the night seining—for it must be said that every effort was made to replace the fish as quickly as possible after they were caught, and with the least possible injury. Since, therefore, the fish have returned to the deep water again in the daytime, a third conclusion can be drawn from the facts: 3) that this migration is a nocturnal-diurnal phenomenon. Figure 14 shows the abundance of the



silversides along seventy-five feet of the north shore of Oconomowoc lake at night, from July 10 to September 24, 1923.

Once the fact of this nocturnal-diurnal migration was established, the next step was to accumulate the facts concerning it: the time at which it occurred both in the morning and at night; the conditions existing when the migration did not occur as well as when it did occur; a correlation between light conditions and migration; chemical conditions of the water in possible relation to the movement, and various other phases of the problem. These will now be discussed.

The fact that young *Labidesthes sicculus* proceed after hatching to a pelagic habitat over deep water, while the adults select a shoal environment was noted by Hubbs (1921), who dismisses the subject with the single sentence: "As these young fishes rapidly grew during the summer, they showed less aversion to shoal waters." It is evident, therefore, that Hubbs has missed entirely the tremendously interesting fact of the nocturnal migration.

In an effort to analyze the change in preference from a suprapelagic habitat to a shoal environment as the fish ages, Hubbs offers a series of possible causes, and rejects them all in turn. It is well to summarize his conclusions briefly, 1) Temperature: this is cast out as a deciding factor as the difference in temperature of the water inhabited by the young over deep water and the adult over shallow water is too small to be effective and is wholly inconclusive. 2) Light: since both adults and immature live very near the surface the light intensity for each would be essentially the same. 3) Oxygen: the amount of oxygen is so nearly the same in both habitats and the range overlaps to such an extent that this is eliminated as the causing factor. 4) Food: is eliminated on the grounds that food is abundant where the species is not found. 5) Protection: is eliminated on the ground that the young were found to "avoid shoals even when other fish were not in evidence" nor "can the seclusion from enemies explain the invasion of the shoals by these young silversides in the *late summer*, nor the exclusive presence there of the adults." 6) Reaction: Hubbs reaches the conclusion that the young have a negative reaction to large objects, hence seek the uniform environment over deep water, and bases his conclusions partially on the fact that the fish "swam away from the boat" as it approached. Had Hubbs hit upon the night movements of the fish, this conclusion would have had to be given up.

The discovery by the writer of this nocturnal diurnal migration puts an entirely different aspect on the problem, which becomes not what causes the young to assume a different habitat from the adult during the early summer and causes them to come back again to the shallow *late in the summer*? but: what are the factors at work that result in the production of this daily migratory phenomenon?

1. Temperature: The writer agrees with Hubbs that there is relatively little difference between the surface temperature over deep water and over the shallows if he specifies *during the day* (which he does not) but with the new turn the problem has taken, a more careful study of temperature relations and conditions must be considered before any conclusions are drawn.

The following table (16) shows a series of temperature readings made over shallow and deep water at 10 o'clock in the morning and again in the same place at 3 o'clock in the afternoon. These readings were made over

TABLE 16  
SURFACE TEMPERATURE OF OCONOMOWOC LAKE OVER SHALLOW  
AND DEEP WATER

Date	Surface temperature over water 1 m deep		Surface temperature over water 16 m deep	
	10 A. M.	3 P. M.	10 A. M.	3 P. M.
6/10/23	18.4	19.5	18.1	18.7
6/20/23	25.3	27.4	25.1	26.7
6/30/23	28.4	29.6	28.2	28.3
7/18/23	27.7	27.9	27.5	27.6
8/1/23	30.8	31.4	29.6	29.8
8/16/23	25.6	25.8	25.4	25.2
9/1/23	30.0	30.9	29.7	29.9
9/24/23	28.4	28.6	28.3	27.8
10/12/23	14.4	14.5	13.6	13.9

locations in which silversides were found, and represent the relative environmental temperatures selected by the adults (1 meter deep) and the immature (over water 16 meters deep). It must be admitted that the absolute differences are slight, but it must also be remembered that fish are very sensitive to change in temperature: Shelford and Powers (1915) report a reaction to a change of  $0.2^{\circ}$ . The table shows conclusively that the adults are located in water that is *uniformly warmer* than the immature; hence the young, on establishing themselves permanently in the shallow water are coming into a region of water that is uniformly a little *warmer*. It does not, however, explain why the young seek the deeper water to begin with.

Turning now to an examination of the temperature conditions over shallow and deep water during the day and night, I find a situation a little more definite, and results a little more decisive. In compiling the following table, two sets of temperature readings were taken, one just under the surface of water 1 meter deep, the other just under the surface of water 16 meters deep. With the aid of an assistant anchored in a row boat over 16 meters of water, I was able to obtain thermal readings of the two localities taken at exactly the same time. These records are tabulated in Table 17.

TABLE 17

TEMPERATURE READINGS OF WATER TAKEN AT FIFTEEN MINUTE INTERVALS DURING THE EVENING OVER SHALLOW AND DEEP WATER: OCONOMOWOC LAKE, 1923

Date	Over water 1 meter deep								Over water 16 meters deep				
	3:00	6:30	6:45	7:00	7:15	7:30	7:45	8:00	3:00	6:30	7:00	7:30	8:00
8/8	24.5	24.3	24.3	24.2	24.1	23.9	23.9	23.8	24.0	23.7	23.4	23.1	23.6
8/10	25.7	25.5	25.3	25.1	25.0	24.8	24.6	24.3	25.1	24.7	24.4	24.1	23.7
8/11	27.2	27.0	27.0	26.8	26.6	26.6	26.5	26.4	26.4	26.1	25.8	25.5	25.1
8/13	30.5	29.9	29.7	29.5	29.2	29.0	29.0	28.8	28.2	27.4	26.8	26.2	25.8
8/14	31.2	31.7	31.4	31.2	30.9	30.7	30.5	30.3	29.4	29.0	28.6	26.2	25.8
8/17	25.9	25.5	25.3	25.3	25.2	25.0	25.0	24.9	24.6	23.7	23.5	23.1	22.7
8/18	29.2	29.0	28.8	28.5	28.4	28.1	27.9	27.7	28.1	27.7	27.3	26.8	26.3
8/22	30.3	30.5	30.4	30.1	30.0	30.0	29.8	29.6	29.8	29.4	29.1	29.0	28.6
8/23	32.1	32.4	32.2	32.0	31.9	31.8	31.6	31.6	31.7	29.9	29.6	29.2	28.8
8/24	30.5	31.0	30.8	30.7	30.4	30.2	30.3	30.1	30.0	29.2	28.7	28.4	28.1
8/26	28.4	28.2	28.0	28.1	27.9	27.7	27.6	27.6	27.5	27.2	26.8	26.4	26.2
9/5	26.3	26.6	26.4	26.3	26.0	26.0	25.8	25.7	25.5	25.0	24.7	24.5	24.2
9/7	23.7	23.6	23.3	23.2	23.0	22.9	22.7	22.4	22.2	21.9	21.6	21.2	20.8

A study of this table will show a number of interesting and important facts. To begin with, it will be noted that there is consistently a slight difference in temperature over the shallow and deep water, and that the shallow water is consistently warmer than is the deep. In the second place it should be noted that the shallow water retains its heat better than does the deep water—that is, the surface water in the shallows tends to cool off less rapidly than does the surface water over the deep. Thus a greater drop in temperature is noted, in a short time over the deep water than over the shallows, and this occurs where the water is already cooler. This is due very largely to the fact that much heat is retained by the sand and bottom material, and tends to replace the heat given off by surface radiation. Therefore, while the difference in actual temperatures is, as has been said, not great, there is a decidedly greater drop over the deep water, and this is the habitat which the young forsake *as the temperature begins to drop*. Correlated with the preceding table, the following tabulation gives further information: the time at which the young silversides arrive in the shallow water. Standing at the end of a pier in 70 cm of water the young were plainly seen coming in from the deep water. The hour of their arrival at this point was noted on the same dates as the data in Table 18 were taken. Characteristic of the shoreward journey is the speed with which the minnows travel: they swim at top speed straight for the shore. Thus, knowing something about the rate of speed with which the fish travel one can figure back and find that the shoreward migration begins at the time the temperature starts to drop over the deep water. Furthermore, be it noted that the minnows arrive *together*, which fact is significant. In from ten to twenty-



TABLE 18.  
TIME OF ARRIVAL OF *LABIDESTHES SICCULUS* IN THE SHALLOW  
WATER DURING THE EVENING MIGRATIONS

(To be considered in connection with Table 26)

Date	Time of arrival	Weather
8/8 .....	7:40	
8/10 .....	7:42	
8/11 .....	7:35	
8/13 .....	7:35	
8/14 .....	7:41	
8/17 .....	7:25	cloudy
8/18 .....	6:55	very cloudy
8/22 .....	7:20	
8/23 .....	7:35	
8/24 .....	7:15	
8/26 .....	7:08	
9/5 .....	6:55	
9/7 .....	6:50	

five minutes the entire silversides population of the lake is inshore. Since there is a lessening gradient in radiation as one approaches the shallower water, it is evident that the fish over the deeper water start their migration first, and move shoreward, picking up the fish nearer the shore as they advance with the drop in temperature, this bringing all the fish into the shallows within a very short interval of time.

With the coming of fall and the cooling of the water, the shallows warm up increasingly more than does the deep during the day, and relatively more heat is stored up in the bottom for radiation during the hours of darkness. Hence the immature fish, on coming into the shallow water to assume the same habitat as the adults, are seeking an environment of *warmer water*. Data indicate that, while the diurnal range of variation may be greater in the shallows than over the deep, the average condition is upward of 3° warmer. Since a factor is of increasing importance as its abundance decreases, this excess of warmth in the shallows must be considered as being important.

One other point needs emphasis in connection with the temperature problem. Observations show that cold water acts as a depressor on the silversides, for the fish are very much less active in winter than in summer. In fact, the fish are so sluggish and slow moving that, when seen under the ice in winter, one hardly recognized the dashing, darting minnow of the summer. The following figures bear out this point:

August 8, 1923. By means of a stop watch the number of vibrations of the pectoral fin were counted. The average of ten counts of 100 vibrations shows the rate of movement per 100 vibrations at a water temperature of 26.2°C as 100 vibrations in 34 seconds.

February 3, 1924. A similar experiment. The average of ten counts of 50 vibrations at a temperature of  $4.5^{\circ}\text{C}$  shows 100 vibrations in 2 minutes and 24 seconds.

This must be taken as an indication of the reduced activity of the fish due to a low temperature, as control conditions were the same in both cases. Hence it can be assumed that a drop in temperature has an effect upon the fish.

In order to ascertain whether or not the fish react to a drop in temperature, ten *Labidesthes sicculus* were placed in a galvanized iron tank four feet long by eighteen inches wide by twelve inches deep. Water taken from their own environment was placed in it, stirred up to give it a uniform temperature, and temperature readings were taken (as well as hydrogen ion concentration readings). The fish were placed in the tank and their movements noted and traced. At the beginning of the experiment the fish traveled consistently the length of the tank, turning back when they hit the ends. As soon as the normal behavior was noted, a piece of ice was suspended in the upper three inches of water at one extreme end and a subsequent tracing of the movement of each of the fish was taken (the experiment being performed separately for each fish). It was found that as the fish approached the ever increasing zone of cooler water they turned back sharply toward the warmer water, and the temperature was taken at the point at which the fish turned back. The results of one of these experiments, which has been selected as typical, is presented (Fig. 15). It will be noted that the fish reversed itself at the first  $0.4^{\circ}\text{C}$  drop in temperature, and that a drop of  $0.7^{\circ}\text{C}$  was sufficient to confine it to one end of the tank. Since the fish used in the experiment were immature individuals measuring 4.5 cm, the conclusion is warranted that the young at least are very sensitive to slight temperature changes. Their sensitivity is not quite as marked as the case of Shelford and Powers (1915) where the reaction occurred at a change of  $0.2^{\circ}\text{C}$ .

The writer can not agree with Hubbs in his statement that the light intensity is the same over deep and shallow water. In fact, when the bottom is clear sand or fine gravel of a light color, the writer believes that there can be no question but that the intensity of the light is *much greater over the shallow water*, due to the reflection from this bottom. Since the bars of Wisconsin lakes are largely light sand, plainly visible because of the clearness of the water to a depth of twenty feet or more, the writer would emphasize the fact that as the fish approach the shore over water becoming increasingly shallower, the light intensity increases in direct proportion to the closeness with which the shore is approached. Hence with the failing light of evening, *if* the fish be positively phototropic, one would expect a shoreward migration in correlation with the decreasing daylight. Does such a correlation exist? I have already mentioned the time at which the

fish come from the deep. By referring once more to table 18, one will find that there is a slow but *very definite* time gradient, from 7:45 on August 8 to 6:50 on September 7. One notes, further, that on cloudy days, when the light intensity is lessened, the hour of inshore migration is notably earlier, as on August 18. These facts, coupled with the known fact that *Labidesthes sicculus* is a surface inhabitant, point to a conclusion that the species is positively phototropic. Is there any further evidence on the question? This brings us again to Hubbs' statement that at night the fish lie motionless as if asleep. Had he happened to visit the lake on a clear moonlight night, he would have seen a sight that would have caused him to alter his conclusions.

During the permanently deep water stage of the life history of the fish the young *do* lie motionless at night—motionless, that is, except for the fin movement necessary to sustain their position. But with the change in habits which propels them shoreward at dusk, certain other changes occur. If the night be dark and calm, with no moon—or at best a new or old moon—the fish come in and behave essentially as they do in the earlier stage of their history over deep water: they lie suspended, motionless. But let the moon be two thirds or more full, and the shallows becomes the scene of one of the most startling activity in the fish world. The silversides seem to go crazy, as if they were moon-struck. They dart about at a most startling speed, dashing here and there, leaping out of the water again and again, bumping into each other, splashing, circling, behaving in a most exaggerated manner. If the water be calm, the surface becomes entirely agitated by their activity so that a myriad of tiny waves dance upon its surface, and the gentle splashing of the “breaks” is the characteristic night sound of the lake. Such activity goes on during the entire night if the light holds. But let the sky become clouded and the moon be hidden, and the activity immediately dies down. That this is a phototropic reaction can not be doubted. If the moon is not sufficiently bright, no activity results; if the moon be full, but so low that the light is refracted from the surface instead of penetrating into the water, no reaction occurs. But let the point of refraction be passed and the activity begins at once. Again, late at night, let the point of refraction be again reached by the setting moon, and activity ceases. It is a phototropic reaction in response to a certain minimum amount of light. Thus one can explain not only their activity on bright moonlight nights, but their incessant activity during the daytime.

A series of simple experiments was designed to see if this activity is a phototropic reaction. On the night of August 10, with no moon present, the fish were up in the shallows, lying quiescent. A bright, focused beam from a pocket flash-light was thrown upon the water. To begin with, there were no fish in the circle of light (two feet in diameter); however, the following results were obtained:



15 seconds after light was thrown, 2 fish were within the circle.									
30	"	"	"	"	"	8	"	"	"
45	"	"	"	"	"	14	"	"	"
60	"	"	"	"	"	23	"	"	"
75	"	"	"	"	"	38	"	"	"
90	"	"	"	"	"	42	"	"	"

Thus, within the short period of a minute and a half 42 fish were attracted into the circle of illumination. This experiment was performed on 32 nights under varying conditions, always with the same general results—the fish *always* came to the light. How strong was the attraction of the light on the fish? By walking out on the pier, a distance of 100 feet, shining the light in the water as I walked, I was able to lead the fish entirely around the pier again and again: they would follow as long as the light was there, with an increasing number of individuals in the procession as new fish found the illuminated area. By sitting in the back end of a row boat with an assistant at the oars, I found that I could lead the fish for quite a distance out into the lake, and once, on a very hot, quiet night, I was able to lead a little school of five silversides entirely across Oconomowoc lake, a distance of seven-eighths of a mile, in three hours and ten minutes. Seventeen fish started the trip; five arrived, the others getting lost en route. On all other occasions the school abandoned the light as deep water was reached, and here it was found that a difference in temperature of 4.3°C existed between the point where they started and the point where they turned back. How far inshore would they follow the light? With the fish normally over 30 cm of water I have repeatedly lead them inshore into water 1 cm or less in depth—up among the stones where there was scarcely enough water to float their slender bodies. Further: I have often had them leap clear out of the shallow water, up onto the dry land, when they were unable to follow the light any farther because of insufficient depth. The conclusion must be drawn that the fish are very strongly positively phototropic and that light intensity plays an important part in their migrations. The writer has been unable to demonstrate any measurable difference in the oxygen content of the upper water and over the deep water which might account for the diurnal-nocturnal movement. Repeated analysis has failed to yield any clue that oxygen is a determining factor in the migration. This conclusion is further borne out by Mr. Juday, who tells me that a demonstratable change in the oxygen content of the water during the day as compared with the night is almost unknown in his experience.

As has been already stated, a change of food habits occurs at the time the shoreward migration begins. Up to this time the food of the young has been almost entirely entomostraca, and entirely plankton organisms. An examination of the stomachs of 250 young *Labidesthes* taken prior to the beginning of the inshore migrations by night, shows the following results:

Entomostraca:	
Cyclops.....	14.5%
Daphnia.....	16.8%
Bosmina.....	35.7%
Other species.....	5.0%
Rotifera:	
Anuraea.....	16.6%
Diatomes, Algae etc.....	8.4%
Unidentified.....	3.0%
<hr/>	
100.0%	

An examination of 250 stomachs of immature individuals taken August 12, at night, while inshore, gives the following results:

Entomostraca:	
Copepoda.....	5.5%
Cladocera.....	10.8%
Ostracoda.....	1.2%
Mysis relicta.....	10.3%
Plant remains.....	9.5%
Insecta:	
Diptera.....	35.2%
Coleoptera.....	9.0%
Larvae.....	22.4%
Unidentified.....	3.2%
Arachnida.....	1.9%
<hr/>	
100.0%	

A comparison between these two tables will show very clearly that a great change accompanies the initiation of the migratory habits of the species, resulting in a much more varied diet when the fish enter the shallow waters. A third series of stomach examinations, consisting of 45 stomachs of adults taken on the night of August 14, gives the following tabulation:

Entomostraca:	
Ostracoda.....	0.5%
Copepoda.....	4.7%
Cladocera.....	12.5%
Plant remains.....	1.4%
Insecta:	
Chironomus larvae.....	58.5%
Diptera, adult.....	21.5%
Miscellaneous.....	3.6%
<hr/>	
100.0%	

Thus there appears a transition from the micro-organism diet to a predominantly insectivorous diet, and this change in the food habits accompanies the change in environment selection. However, since entomostraca are

still eaten commonly by the adults, and since insect food is notably absent over the deep water of the lake, it must be assumed that the change in food habits is a secondary one, a *result* of the changing of the environment, rather than a *cause* of it. It is a well known fact that the food habits of a species undergo radical changes as the fish grow; this has been pointed out by Forbes, Turner, Pearse, and others, but in no case has it been shown that this change causes migration or in any way disturbs the distribution of the species. However, the consideration of the cisco later furnishes an example of just this type of phenomenon. The case of *Labidesthes* is different, and it is necessary to consider the change in diet as characteristically an accompanying phenomenon, not a causing one.

There can be no doubt but that the habit of the young silversides in assuming a pelagic environment over deep water is a very great protection to the species. As they are for the most part the only inhabitants of these waters, they escape the very keen competition existing in the shallow water. Their very small size would make them ideal food for the dozens of species of larger fish which feed in the shallows along the shore. As it is their enemies are reduced to a minimum as long as they remain over the deep water. In this habitat they are preyed upon by the following species: *Clidonias nigra surindmensis*; *Sterna hirundo*; *Lepisosteus osseus*; *Leucichthys artedi* which occasionally comes to the surface and captures them; *Micropterus dolomieu*; *Micropterus salmoides*. The last two named make occasional raids into the region and capture a good many silver sides.

However, once the species begins its shoreward movement, the number of enemies increases tremendously. I have found remains of silversides in the stomachs of the following animals which captured the fish while in the shallow water:

*Micropterus dolomieu*; *Micropterus salmoides*; *Amiatus calvus*; *Esox lucius*; *Amploplites rupestris*; *Lepomis cyanellus*; *Lepomis incisor*; *Eupomotis gibbosus*; *Roccus chrysops*; *Perca flavescens*; *Esox vermiculatus* (Fox river only); *Leucichthys artedi* (during spawning season only); *Botaurus lentiginosus*; *Ixobrychus exilis*; *Ceryle alcyon*; *Mergus serrator*; *Necturus maculatus*; *Chelydra serpentina*; *Natrix sipedon*; *Cambarus* spp.; and *Mustela vison*.

Thus it becomes evident that the species is tempting fate when it comes inshore, and that this temptation results in wholesale destruction of the species is evidenced by the curve showing the abundance at night along the shore (Fig. 14). Here is shown the tremendous decrease in numbers that occurs between August 6 and September 6, when the silversides are reduced to such an extent that they no longer offer the wholesale food supply to their competitors. From these facts two conclusions can be drawn: 1) that the pelagic habitat is a great protection for the young as long as they remain in it; and 2) that the change from the deep to the



shallow water environment is not due to enemies in the deep. Hence protection can not account for the migration toward the shore.

The suggestion of Hubbs that the species seek the deep water as an avoiding reaction against large objects falls down when the species is found returning to the shallows under cover of twilight and associating itself more closely with large objects than any fish with the exception of those characteristically bottom thigmotactic forms such as many of the species of *Boleosoma*, *Cottus*, *Etheostoma*, etc. Since the fish return to their deep water station again during the day, it would be hard to account for this reversal of their reaction if the behavior were merely a negative response to large objects.

In order to determine in the laboratory whether the young fish tend to avoid large bottom objects, the same tank used in the work on changing temperature was used. This time three large stones were placed near one end, and the fish permitted to swim around in the tank. The results as shown in figure 16 indicate that the fish pay no attention to the presence of large objects on the bottom. In the case of a piece of floating wood, however, the fish show a marked aversion to its vicinity. This however, is not surprising, and can be considered as nothing more than a normal reaction to an object in the path of progress. It could hardly be expected that a fish or any other animal would do anything other than avoid such an object.

This brings us to the last of the factors investigated by the writer as a possible cause of the migrations which *Labidesthes* performs, the change in hydrogen-ion concentration of the water. It was previously noted that there is a slight change in the H-ion concentration of the lake water from top to bottom, the pH readings (colorimetric) being higher at the surface than at the bottom (see table 3) indicating a lesser (more alkaline) condition near the surface. Inasmuch as the silversides is confined to the surface waters, it is these surface conditions that are important. The question under consideration becomes: is there any change in the H-ion concentration over the deep water that could cause or initiate the shoreward movement as evening approaches.

With the aid of the assistant, a series of readings of H-ion concentrations were made over the shallow and deep waters, a duplicate, checked series of phenol red indicators being used. Two samples of water were taken in each case, and if there occurred a material difference between the two readings, a third was immediately taken. In order that the light conditions remain constant throughout the work both day and night, a small black box was fixed to the end of a pocket flashlight, and the light sent into the box through a pale blue glass, to give as nearly a white light as possible. Both batteries were checked at the beginning and end of the work each day. A hole in the top of the box permitted the insertion of the

tube containing the sample to be examined and a vertical slit made possible a clear reading under constant illumination. This precaution regarding the light was made necessary as it was found that very deceiving results were obtained as the light intensity diminished, the weakening light giving higher readings than normal light, thus leading to conclusions wholly erroneous and misleading. The results obtained over a period of a month are given in table 19.

TABLE 19  
CHANGES IN HYDROGEN ION CONCENTRATION IN THE EVENING  
OVER SHALLOW AND DEEP WATER: OCONOMOWOC LAKE, 1923

Date	Over shallow water								Over deep water				
	3:00	6:30	6:45	7:00	7:15	7:30	7:45	8:00	3:00	6:30	7:00	7:30	8:00
8/8	8.0	8.0	7.9	7.8	7.8	7.65	7.6	7.6	7.8	7.8	7.6	7.6	7.5
8/10	8.1	8.0	7.95	7.9	7.8	7.7	7.7	7.65	7.8	7.75	7.7	7.6	7.55
8/11	8.0	8.1	7.96	7.95	7.85	7.7	7.65	7.6	7.7	7.7	7.65	7.6	7.5
8/13	8.2	8.0	7.9	7.9	7.85	7.75	7.6	7.6	7.9	7.8	7.6	7.6	7.5
8/14	8.2	8.1	7.95	7.95	7.85	7.8	7.8	7.7	7.8	7.75	7.7	7.6	7.6
8/17	7.9	7.8	7.8	7.7	7.65	7.65	7.6	7.7	7.7	7.65	7.55	7.5	7.45 cloudy
8/18	7.8	7.8	7.8	7.75	7.65	7.6	7.6	7.6	7.7	7.65	7.6	7.55	7.5 cloudy
8/22	8.0	7.95	7.9	7.9	7.85	7.8	7.75	7.7	7.8	7.7	7.6	7.55	7.5
8/23	8.2	8.1	7.9	7.85	7.8	7.7	7.7	7.6	7.9	7.85	7.75	7.6	7.55
8/24	8.0	8.0	7.9	7.85	7.8	7.7	7.65	7.6	7.8	7.7	7.6	7.5	7.45
8/26	7.9	7.8	7.8	7.7	7.7	7.65	7.6	7.6	7.7	7.65	7.55	7.5	7.5
9/5	7.8	7.7	7.65	7.65	7.6	7.6	7.6	7.55	7.6	7.65	7.6	7.5	7.5
9/7	7.8	7.8	7.75	7.7	7.7	7.6	7.6	7.55	7.65	7.6	7.5	7.45	7.45

From this table certain facts become clear: 1) that the H-ion concentration over the shallow water is lower (pH higher) during the day than over the deep water. This is undoubtedly due to the great activity of the shallow water vegetation, which during the day is giving off oxygen and taking on carbon dioxide. 2) It is to be noted that with the coming of darkness the H-ion concentration increases, as indicated by the decreasing amplitude of the figures. 3) The change in H-ion concentration is greater along the shore than over the deep water. This again is due to the plant activity and the reversal of the photosynthetic process; oxygen is now being taken up and carbon dioxide given off, thus increasing the acidity and increasing the H-ion concentration. 4) Both the shallow and deep water reach a stage of more or less stable equilibrium with the pH of the shallow water higher than that over the deep. 5) Finally, *Labidesthes sicculus* moves toward the higher pH value as the change begins to occur over the deep water. That the species is sensitive to changes in the H-ion concentration of the water is further made clear by a series of laboratory experiments to be discussed.

So far I have considered only the shoreward migration of the evening, and have said little as to the outward migration of the morning. This morning movement is very much harder to study, as it is less definite, less of a mass movement, than is the evening migration, and this in itself indicates what might be termed "reluctance" on the part of the fish to leave the shallows, and also because the departure of a few fish from a great school is less easily noted than the first arrivals in an area theretofore free of the species. The region into which the evening movement comes is relatively limited; that into which the morning migration goes is relatively unlimited. Yet a study of the H-ion concentration changes during the early hours of dawn gives a very good clue as to the cause of this second phase of the daily shifting. The results of the changes in H-ion concentration along the shore and over the deep water, made in the same way as the night readings, are given in Table 20.

TABLE 20

CHANGES IN HYDROGEN ION CONCENTRATION IN THE MORNING  
OVER SHALLOW AND DEEP WATER OCONOMOWOC LAKE, 1923

Date	Over shallow water:							Over deep water:						
	3:00	3:30	4:00	4:30	5:00	5:30	9:00	3:00	3:30	4:00	4:30	5:00	5:30	
8/9	7.6	7.65	7.65	7.7	7.8	7.85	7.9	7.5	7.5	7.6	7.65	7.7	7.7	
8/10	7.6	7.65	7.7	7.8	7.85	7.85	8.0	7.5	7.5	7.6	7.65	7.7	7.8	
8/11	7.55	7.65	7.7	7.75	7.85	7.9	8.1	7.5	7.5	7.5	7.6	7.7	7.75	
8/14	7.6	7.7	7.75	7.8	7.85	7.85	8.0	7.55	7.6	7.6	7.7	7.75	7.8	
8/17	7.65	7.65	7.7	7.7	7.7	7.75	7.9	7.5	7.5	7.55	7.6	7.65	7.7	
8/18	7.6	7.6	7.6	7.65	7.65	7.7	7.9	7.5	7.5	7.5	7.55	7.6	7.65	
														(cloudy)
8/22	7.65	7.65	7.75	7.8	7.85	7.9	8.1	7.55	7.6	7.6	7.65	7.7	7.8	
8/24	7.6	7.65	7.7	7.75	7.85	7.95	8.0	7.5	7.5	7.55	7.6	7.6	7.7	
8/26	7.55	7.6	7.65	7.75	7.75	7.85	7.95	7.45	7.5	7.5	7.55	7.65	7.75	
9/5	7.55	7.55	7.55	7.60	7.65	7.7	7.8	7.45	7.5	7.5	7.55	7.6	7.7	
9/15	7.55	7.55	7.55	7.55	7.6	7.65	7.8	7.45	7.5	7.5	7.5	7.65	7.7	

As compared with Table 19 showing the evening changes, certain marked and important differences are to be noted. Conspicuous among these is the fact that the H-ion concentration along the shore begins to change considerably earlier than over the deep water, as indicated by the rise in the pH values as early as 3:30 on August 8. The fact that the pH values for September do not change as early as those in August must be explained as being due to the light conditions as affecting the respiratory activity of the aquatic vegetation. It is a well known fact that photosynthesis takes place in the presence of very little light; hence the night intake of oxygen and output of carbon dioxide are reversed in the early morning hours long before the sun gets up, resulting in the output of oxygen



and intake of carbon dioxide. With the intake of  $\text{CO}_2$  the change in the H-ion concentration of the water begins and this is indicated by the slowly rising amplitudes of the pH values, showing an increase in alkalinity. Since the surface water over the deep is less abundant in photosynthesizing organisms, the larger aquatic plants being entirely absent, the change in pH values is measurably slower. It is to be noted further that on cloudy days (August 18) the pH values change more slowly and at a later hour, due to the absence of sufficient light to start the photosynthetic processes of the water plants.

The morning off-shore migration of the silversides starts with a definite change in the H-ion concentration of the shoal water. This becomes evident if one compares the different pH values with the hour at which the fish start out.

TABLE 21  
HOUR OFFSHORE MIGRATION BEGINS AND pH OF WATER AT THAT TIME

Date	Time of start of outgoing	pH of the water at that time
8/9	4:20	7.65
8/10	4:05	7.7
8/11	4:08	7.7
8/14	3:48	7.65
8/17	3:58	7.7
8/18	5:20	7.65
8/22	4:10	7.75
8/26	4:22	7.7
9/5	3:55	7.65
9/15	5:10	7.6
Average:		7.68

Thus it is seen that the fish leave the shore as the pH reading reaches 7.65 to 7.7, the average being 7.68, which can not be read by the colorimetric method. This gives a clue to the cause of the morning movement: it is an avoiding reaction to a higher pH reading, that is, to water of increasing alkalinity. Since the water in the shoal environment shows a higher pH reading during the day than does the water over the deep, and since the water over the deep shows a lower pH value at night than does the shallow water, it must be assumed that the fish are reacting negatively to a high pH value and negatively to a low pH value, indicating a marked sensitivity to H-ion change and a limited range of tolerance. This conclusion is borne out in a series of laboratory experiments. It is impossible to account for the morning migration by light, temperature, food, oxygen or protection, but one can account for it as a reaction to changes in the hydrogen-ion concentration of the water.

In order to ascertain the pH preferences of the fish the galvanized iron tank was again used. This was filled with water and well mixed so as to give a uniform pH value throughout the tank. The fish were placed in the tank and their normal movements noted. Then the pH readings were taken at different points in the tank to make sure that the environment was uniform. At one end of the tank a small amount of acetic acid was added, this lowering the pH readings as the H-ion concentration increased with the increased acidity of the water. The behavior of the fish was noted and the pH of the water was taken at the point where the fish turned back in its avoidance reaction. The results of this procedure are given in figure 17. The fact that the fish react against a slight increase in the acidity of the water is shown by their returning to the less acid end of the tank as soon as they come in contact with the increasing zone of water of a higher acidity. The change from the pH of 7.9 is noted by the fish at once, and the pH value of 7.7 and 7.65 are evidently the critical points. The fish does the best it can to avoid the increasing acidity by retreating before the advancing zone of pH 7.65, and the experiment ends with the fish flat up against the end of the tank farthest away from the acid, with further retreat impossible.

Essentially similar results were obtained by the use of carbonate instead of acid, thus increasing the alkalinity of the water. These results are given in figure 18. It is evident from a glance at this figure that the fish avoid water of a higher pH than 8.2 if possible. It is further evident that their avoidance to increasing alkalinity is less decided than to an increasing acidity as evidenced by their frequent lingering along the advancing pH 8.2 line. As in the case of acidity, the fish are evidently doing their best to avoid the radical change in pH until retreat is impossible longer. In this connection it is well to note that the critical point is very close to pH 8.2, which is also the pH value of normal sea water. This may be significant when one recalls again that this is a fresh water representative of an otherwise strictly *marine* family, and becomes more marked when one compares the reactions against higher alkalinity and higher acidity; it is to be noted that the reaction against higher acidity is less decisive.

In order to see how the fish would react in a tank with high alkalinity at one end and high acidity at the other, a third series of experiments was run under combined conditions. The results are very similar to those of the two preceding experiments combined. The fish retreat before increasing acidity and tolerate greater alkalinity in preference to greater acidity, as shown in figure 19. It will be seen that as long as any real choice was possible, the fish chose a pH value very close to 7.7.

From these experiments it must be concluded that: (1) the fish are very sensitive to pH changes in the water; (2) their range is from pH 8.3 to pH 7.5, with the optimum approximately 7.65 to 7.7; (3) the experi-

mental results check very closely with the behavior of the fish in nature; (4) there is a greater tolerance for increased alkalinity than for low alkalinity or acidity; and (5) the experimental data bear out the assumption that the early morning change in the hydrogen-ion concentration of the shore water is sufficient to cause the offshore migration of the species at that time.

This sensitivity on the part of the silversides suggested an experimental study of the pH of the blood of the species in an effort to ascertain whether or not there is a correlation between the pH preference of the fish and the pH of the body fluid. The procedure followed was that of Levy, Rowntree and Marriott. Celloidin sacs (or dialyzing tubes) were made according to their method, and stored until used in normal salt solution. The idea of the experiment was to obtain an amount of blood of the fish and dialyze this blood through the celloidin sac suspended in normal salt solution. The dialysis excludes from the liquid outside of the sac both proteins and coloring matter, but permits the free outflow of hydrogen ions. As the amount of blood obtainable from a single silversides is small—even in the case of the adults—it became necessary to use a number of fish in each experiment. A thin hypodermic needle was inserted directly into the heart of the fish, this being rendered a simple operation by the transparency of the fish. The blood drawn out was placed in a small test tube, the mouth of which was covered with a rubber membrane to exclude the air. In an effort to exclude the maximum amount of air, the test tube was filled with normal salt solution before the rubber membrane was put on, and the liquid was then drawn off by means of a hypodermic needle inserted through the membrane. When 3cc of the blood was obtained, the blood was transferred to the celloidin sac and suspended in a slightly larger glass test tube containing 3cc normal sodium chloride solution. After standing for five minutes, the pH of this solution was read. This experiment was performed on both immature and adult fish with the following results:

TABLE 22

TESTS OF BLOOD OF YOUNG AND ADULT *LABIDESTHES SICCULUS*

No. Fish used	Young		pH	No. fish used	Adults	
	Av. length			Av. length	pH	
14	2.4		7.7	8	7.6	7.8
17	2.0		7.7	7	7.62	7.85
18	2.1		7.75	10	7.61	7.85
Average:			7.71			
						7.83

These results are interesting and instructive, for they show that the pH value of the blood has undergone a modification as the fish mature. It



shows that the pH of the blood of the young fish is lower than that of the adults, and it will be remembered that the young fish on coming into the shallow water, are entering a region of higher pH values: the older they are the more permanently do they select the shallow water with its higher pH values, and the older they are the higher the pH of the blood becomes. Thus the change in habitat selection appears as a reaction to a physiological change in the body which results in a change in the H-ion concentration of the body fluid.

#### THE ADULT FISH

Once the fish establish themselves inshore toward the end of the summer, their lives assume a much more even and less exciting level. With the coming of the cold weather and the coincident cooling of the water, the activity of the species becomes conspicuously reduced. The species remain inshore all winter, with the exception of a slight tendency to wander about, due probably to the uniform conditions of the water. Occasionally they drift slowly through the openings in the ice where the cisco fishermen are at work over the deep water. Much more frequently, however, they are seen along the shore over water up to two meters deep where the ice cutters have cleared their fields. Movements are slow and sluggish and in marked contrast to the summer activity as already noted. The food habits revert back to those of the immature, principally because of the almost total absence of other food in the upper stratum of water. In fact, it is quite a difficult task at times to obtain sufficient fish during the winter to get a fair idea of what they are feeding upon, so scantily do they appear to feed. This is borne out by the fact that growth ceases entirely and the fish are living on a maintenance ration only. With the coming of spring and the warming of the water, the normal activity slowly returns and the species goes back to its insectivorous diet. With this increase in activity and the excess of rations above the point of mere maintenance, a new growth period is initiated and the fish attain their full size during the early summer (Figs. 11, 12). In June comes again the spawning season, the young of the previous summer go through their breeding performances, and the life cycle begins over again in the new generation.

As to the old generation, their fate is apparently sealed, for they die before the second winter is upon them. The problem of their death and its causes has not been attempted by the writer. It is evident, however, that the adults die sometime during the last half of their second summer, for neither Hubbs nor the writer has ever seen a silversides showing two annuli on the scales. In an examination of 478 adults, no second winter ring has ever been found. Then too, as the summer advances, the adults grow notably less common. On the night of July 18, 1923, I was able to pick up 26 adults along a few hundred feet of shore line in a few minutes;

on September 12 I was able to get only 5 after several hours of search over a considerably more extended area. By adults are meant, of course, those individuals which have passed through one winter and have spawned once. Therefore it must be concluded that the old fish die at the age of about fifteen to seventeen months, breeding but once and leaving it at that to the young to carry on the species.

#### SUMMARY OF RESULTS ON LABIDESTHES

1. *Labidesthes sicculus* is the only fresh water representative of the marine family Atherinidae found in Wisconsin waters.

2. The fish are found only at the surface of the water, and under no conditions will they descend below a meter from the surface.

3. The spawning habits are described and data are presented which show that the deposition of eggs begins when the water reaches a temperature of 20°C, with the optimum temperature of 23°C.

4. The eggs hatch in approximately eight days at 23°C.

5. The embryological development is unknown.

6. On hatching, the young fish migrate at once away from the shore, and assume a position over the deep water, living at all times within a few centimeters of the surface film while the adults remain permanently inshore.

7. After hatching, the young grow very rapidly, and complete data for the growth of the species are presented.

8. When the young reach an average length of 1.4 cm, they migrate into the shallow water each night and before sun-up they migrate back again to their pelagic habitat over deep water.

9. Data are presented which show that this inshore movement is coincident with a drop in temperature of the surface water over the deep water, as well as with a change in the hydrogen-ion concentration of the water at that stratum.

10. Evidence is presented which shows that the shoreward migration is in the direction of increasing light intensity, indicating a positive phototropism.

11. The fish are constantly active during the day; at night, if it be dark, the fish remain quiescent over the shallows.

12. If the night be light, due to a nearly full moon, the fish show extreme activity, leaping out of the water and displaying unparalleled vivacity.

13. This activity can be induced on a dark night by introducing a spot light on the water, proving the species to be positively phototropic.

14. Further proof of this phototropism is presented by the fact that the young can occasionally be lead entirely across the lake, a distance of nearly a mile, as they follow a light; at all times they can be led to a point

where change in hydrogen-ion concentration and low temperature overcome the phototropic reaction and cause the fish to turn back. The fish will even leap out of the water upon the dry land in an effort to follow the light.

15. This night activity is due to moonlight of a certain intensity and it occurs only when the light penetrates into the water.

16. As the season goes on, a marked decrease in the abundance of *Labidesthes* along the shore is noted.

17. Data are given which show that the species in coming into the shallows is attempting to maintain a pH equilibrium of approximately 7.7.

18. Further data show that the species migrate to the deep water in the morning with the rising pH value of the water due to the photosynthetic activity of the shallow water vegetation.

19. Experimental data show that the species avoid and react to a drop of 0.4°C in the temperature of the water.

20. Further experimental data show that the fish avoid both increasing acidity and increasing alkalinity, but that the aversion to a higher alkalinity is less marked than to a lower alkalinity; that a pH of 8.2 is tolerated without resistance, and it is noted that this is the normal pH for sea water.

21. Experiments on the blood of the fish show that there is a difference in the pH values of the blood of young and adults; that of the young is pH 7.71; of the adult 7.83.

22. The migrations of the fish are therefore correlated with the hydrogen-ion concentration of the blood: the young fish with the low pH values remain in that portion of the lake having the lowest pH readings, as they begin to mature and the pH of their blood changes, they begin to come into water having a higher pH value.

23. The food habits of 550 individuals of all ages were studied. The young are plankton eaters; as they begin their shoreward migrations a change in food habits occurs and insect food tends to replace the plankton organisms; that the adults are very largely insectivorous during the summer, but tend to revert to the food habits of the immature during the winter.

24. Examination of 478 adults has shown the presence of but a single annulus on the scales, from which, together with the decreasing abundance of the adults in late summer, it must be concluded that the individuals live for but fifteen to seventeen months.



THE CISCO *LEUCICHTHYS ARTEDI* (LE SUEUR)

## INTRODUCTION AND DESCRIPTION

Among the most abundant of the food fishes of the great lakes is the Lake Herring or Cisco, *Leucichthys artedi* (Le Sueur). Either this species or a variety of it is an inhabitant of all the great lakes and is particularly abundant in Lake Michigan, the southern end of which marks the southern limit of the fish. It is found also abundantly in most of the larger lakes of Wisconsin, and must be considered as a characteristic fish of the deeper inland bodies of water of that state. In southern Wisconsin, within the limits of Waukesha county, the species has been taken in the following lakes: North, Pine, Nagawicka, Okauchee, Oconomowoc, Fowler, La Belle, Upper and Lower Nashotah, Upper and Lower Nemahbin, Silver and Dutchman's. In the largest lake of the county, Pewaukee, the species does not occur as the lake is too shallow to accommodate it.

The family Salmonidae comprises two great groups of fishes, the white fishes or Coregoninae and the salmon and trout series, the Salmoninae. Three genera make up the Coregoninae: Coregonus, the true whitefish; Stenodus, a peculiar trout-like whitefish from the Mackenzie river, a genus represented by a single species, *mackenzii*; and Leucichthys, the lake herring or cisco, represented by about ten species, which may or may not prove valid. The exact number of species is not known, as the ciscos are extremely variable; hence it is probable that many of the present so-called species will be shown to be synonymous. Variability is, as a matter of fact, characteristic of the whole family. This variability, taken in connection with the fact that no salmoid fish is known in a fossil condition except from very recent deposits, forces the conclusion advanced by Günther that the group is of recent origin. Certain it is that, though the ciscos from the above mentioned lakes are all alike in essential structures, if one is familiar with the fish from the different lakes, it is possible to sort out a mixed collection according to the lakes from which the fish came on the basis of variations in color or body proportions, length and depth of caudal peduncle, and other characters. Yet the writer believes that, until a much more careful study of the genus Leucichthys is made than has appeared to date, all the fish should be considered as merely local environmental variations of the single species *Leucichthys artedi*. (Fig. 3.)

*Leucichthys artedi* was described by Le Sueur in 1818 from specimens taken in Lake Erie, near Buffalo, under the name of *Coregonus artedi*. In

1850 Agassiz separated the herrings from the white fish, placing them in the genus *Argyrosomus*. However, it has been found that the name *Argyrosomus* is preoccupied, having been given to a group of French species by de Fougères in 1834. In 1874 Dybowski gave the generic name of *Leucichthys* to a group of Siberian species of the genus *Argyrosomus* Agassiz, creating *Leucichthys omul* and *L. tugun*. These become the type, therefore, of the genus *Leucichthys* to which the American species belong. The first to recognize the true situation was Gill, and he is followed by Jordan and Evermann (1911) who apply the name *Leucichthys artedi* for the first time. A similar confusion exists regarding the species which occur in Wisconsin, but until the genus is entirely and thoroughly reviewed little can be done to straighten out the matter. Jordan and Evermann (1896) refer to the cisco of Oconomowoc lake as *Argyrosomus artedi* in their next review of the group (1911) they call it *Leucichthys cisco* the type being from Lake Tippecanoe, near Warsaw, Indiana. However, they state that it is simply a land-locked *artedi*, structurally indistinguishable from it. In view of this confusion, the writer is inclined to follow the original work of Jordan and Evermann, and calls the fish *Leucichthys artedi*, it being understood that the species in question is the common cisco of Oconomowoc lake, Waukesha county, Wisconsin.

*Leucichthys artedi* is described by Jordan and Evermann as follows: "Head  $4\frac{1}{2}$ ; Depth  $4\frac{1}{2}$ ; eye 4 to  $4\frac{1}{2}$ ; D. 10; A. 12; Scales 8-75 to 90-7; 10 rows under base of dorsal; vertebrae about 60. Body elongate, compressed, not elevated. Head compressed, somewhat pointed, rather long, the distance from occiput to tip of snout usually a little less than half the distance from occiput to dorsal fin. Mouth rather large, the maxillary reaching not quite to the middle of the pupil,  $3\frac{1}{4}$  to  $3\frac{1}{2}$  in head; mandible  $2\frac{1}{2}$ . Preorbital bone long and slender; suborbital broad. Gill rakers very long and slender, 15-17-28 to 34, the longest  $1\frac{1}{2}$  in eye. Dorsal fin high, its rays rapidly shortening. Bluish black or greenish above; sides silvery, scales with dark specks; fins mostly pale, the lower dusky-tinged. Length 12 inches. Great lakes and neighboring waters. An active, voracious fish. Represented in numerous small lakes in Indiana and Wisconsin (Oconomowoc, La Belle) by the slightly modified *Argyrosomus artedi cisco* Jordan." The latter is differentiated from the regular *artedi* by no other fact than that it is a bit smaller and living in deep water. The only lake in southern Wisconsin which contains ciscos as small as 12 inches when mature is Pine lake. Until the last few years, Oconomowoc lake averaged fish 16 inches long or more, and weighing up to  $4\frac{1}{2}$  pounds. Beyond the descriptions of various species and subspecies of the genus, the ichthyological literature is entirely silent concerning the cisco of the inland lakes, and other than the fact that they "spawn in shallow water in November," notes on the food habits of other species, notably *L. birgei* Wagner as

described by Pearse (1921), and the statement also by Pearse that the cisco is a bottom seeking form (based on the independent work of Pearse and Cahn) nothing has been published regarding the ecology of the fish. Two studies of the Lake Erie cisco (*Leucichthys* sp., but not *artedi*) have recently been published by Clemens (1922). This report is, therefore, the first contribution to a life-history study of the cisco, *Leucichthys artedi*.

The following ecological study was begun in 1915 at the University of Wisconsin on the species inhabiting Lake Mendota, which is the same as that occurring in the other southern Wisconsin lakes. In 1917 the study was begun in Oconomowoc lake and in other lakes in Waukesha county, and has been carried on each summer since then (except 1919, when the writer was in France), and at intervals during each winter. During the summer the fish have been caught in numbers by means of gill nets; during the winter with hook and line. Live fish were kept in the large concrete tank in the vivarium at the University of Wisconsin during the winter of 1916, and their reactions and habits were under constant observation. Thousands of fish have been examined for age, weight, length, food, parasites, and these examinations and observations are the basis of this report.

#### BREEDING HABITS

The cisco is essentially a deep water fish, spending its life in the deepest part of the lakes during such times of the year as conditions (oxygen content of the water, etc.) permit. This is of interest in view of the statements of Ward, Milner and others to the effect that the fish are surface species in the Great Lakes. This is one of the differences that have been mentioned as separating the small lake forms from the Great Lakes fish. Thus one finds the fish in the deep water of Oconomowoc lake following the fall over turn when the winter conditions of the lake are established. The thermocline has descended and a uniformity of oxygen content exists throughout the water, making the entire lake available to the fish. However, the part selected by the fish is the cold water of the bottom. As the thermocline descends, the temperature of the water also drops slowly. As the water of the lake cools and approaches a mean temperature of 5.0°C (41°F) the fish show the first signs of the breeding migration, and approach the shallower waters near the sand bars. With the continued cooling the fish approach the shore still more closely, surmounting the bars and appearing in water from one to three meters deep. If rivers enter the lake, the fish may ascend them. Thus, the ciscos come up the Oconomowoc river from Fowler lake, only to be stopped by the locks and dam at the outlet of Oconomowoc lake. Much of this trip is made in water not over 1 m in depth and still shallower water is encountered by the Oconomowoc lake ciscos in their ascent of the Oconomowoc river toward Okauchee



lake. True, the ascent of the rivers is a rheotropic reaction, but too much weight must not be placed on this because of the fact that in reality only a small part of the fish of the lake actually travel up the streams, the majority of the individuals, all of whom had the same chance to go upstream, content themselves with approaching the shore and lay their eggs there. This is perhaps well for the species, for it is very doubtful, indeed, if any of the eggs laid in the shallow water of the rivers ever hatch and return young fish to the lake: there are too many voracious small fish seeking to devour the eggs and fry.

The first fish to reach the shallows are the males, and they are functionally ripe when they arrive. These early arrivals strip easily and microscopic examination shows abundant normally active spermatozoa. The first arrivals usually come in at night, but this is not always the case. They swim leisurely about, occasionally wandering toward the deep water, but show a distinct tendency to follow the shoreline. This movement exhibits no co-ordination as to direction, about equal numbers traveling in each direction, which is in marked contrast to the behavior of the fish when they are "schooled up" in the deep water. The arrival of the males precedes that of the females by from two to four or five days. As the controlling factor for the arrival of each sex is the water temperature, no definite statement can be made as to the intervening time; it depends on the weather and the resulting influence on the water temperature. With the arrival of the females the breeding begins. Several males follow behind a single female at a distance of about one foot, the number of males to a female varying considerably. The first females to arrive may have over a dozen males in attendance, while later on two males is more usual. The actions of the fish are at all times slow and deliberate; there is no chasing or darting about, no evidence at all of excitement or pugnacity. The deposition of eggs takes place in water varying from one to two meters in depth, and the region is free from heavy aquatic vegetation. The female descends to within six or eight inches of the bottom as the eggs are deposited, the male following close behind and along side, his head about even with the anal opening of the female. It is not at all infrequent to find two males present during the fertilization process. As the eggs appear, coming from the female in a thin cylindrical band, the males discharge the spermatozoa freely in the water, forming a conspicuous milky cloud as they swim slowly along. The spawning fish does not cease swimming, with the result that the total egg complement is well scattered over a considerable area. The eggs are slightly viscous, the result being that they become fixed to the rocks, vegetation or debris on the bottom, where they remain during their developmental period.

As to the conditions surrounding the nuptial migration, they have been carefully worked out. It was early discovered that the arrival of the

fish from the deep water is in a direction perpendicular to the shore, hence it proved a simple matter by means of gill nets, to follow the movements of the incoming ciscos, and to make temperature, oxygen and hydrogen ion readings in connection with the progressive migration stages.

Table 23 gives the results of the temperature readings made during the spawning season of 1916, which is typical of those made in Oconomowoc lake in 1917, 1918, 1921, 1922, and is graphically represented in figure 20.

TABLE 23

THE SPAWNING PERIOD OF THE CISCO IN LAKE MENDOTA AT MADISON, WISCONSIN, IN RELATION TO THE TEMPERATURE OF THE AIR AND WATER

Date	Temperature of Air                  Water		Number of ciscos caught	Male	Female
Nov. 15	— 4.5	8.8			
16	— 0.5	8.8			
17	2.0	8.6			
18	5.0	8.8			
19	1.0	8.1			
20	1.0	7.7			
21	— 3.0	7.0			
22	— 5.5	6.4			
23	0.0	6.2			
24	2.7	6.7			
25	11.0	6.2			
26	7.0	6.2			
27	2.4	6.2			
28	1.0	5.8			
29	— 4.5	5.5			
30	— 3.0	5.2			
Dec. 1	— 1.0	5.0			
2	— 4.5	4.5			
3	— 1.0	4.3	3	3	0
4	— 1.0	4.3	10	10	0
5	— 0.5	3.8	10	8	2
6	— 1.5	4.0	21	9	12
7	1.0	3.7	38	11	17
8	1.0	3.3	39	10	19
9	— 22.0	3.4	14	8	6
11	— 2.5	3.3	5	2	3
10	— 2.0	3.0			
12	— 2.0	2.6			
13	— 7.4	2.5			
14	— 11.5	2.3			
15	— 8.3	2.0			
16	— 9.0	1.7			

This gives certain definite information regarding the conditions which precede and accompany the breeding of the cisco. Here it is seen that the

males come into the shallows when the water first reaches a temperature of 4.3°C; that the females arrive when the temperature has dropped to 3.8°C and that the spawning season is at its height with the water at from 3.6°C to 3.3°C; and finally, that the season is abruptly over as the water drops below this figure. Table 24 gives the conditions during other years.

TABLE 24.  
CONDITIONS UNDER WHICH CISCO SPAWNED FROM 1916 to 1921

	1916	1917	1918	1919	1921
	M	M	O	O	O
First ♂ in shallows	Dec. 3	Nov. 29	Nov. 30	Nov. 28	Nov. 26
Temperature water:	4.3	4.4	4.4	4.3	4.3
First ♀ in shallows	Dec. 5	Dec. 2	Dec. 2	Nov. 30	Nov. 29
Temperature water:	3.8	3.9	3.8	3.7	3.65
Maximum spawning:	3.3	3.5	3.5	3.4	3.3
Spawning over:	3.0	3.1	3.0	3.0	3.1

M=Lake Mendota    O=Oconomowoc Lake

From these data it must be concluded that the critical temperature at which the male cisco enters the shallows is very close to 4.3°C; for the female it is 3.8°C; and that the optimum temperature is between 3.3° and 3.5°C.

As to the ratio between the sexes, it appears that the males outnumber the females to some extent, as shown by the following:

No. ciscos examined	Lake	Males	Females
163	Mendota	101	62
744	Oconomowoc	429	315
907		530	377

This is in the ratio of 100 males to 71.2 females. This difference can be explained by the greater mortality among the females during the late summer, as will be seen later.

The number of eggs laid by the female varies considerably, depending of course upon the size and age of the fish. By the water displacement method the following count of the number of eggs laid by a single female was obtained:

Amount of water displaced by eggs.....	46.5 cc
To displace 1 cc water (av. 5 counts).....	329 eggs
Total number of eggs.....	15,238
Weight of female before stripping.....	465 grams
Weight of female after stripping.....	405 grams
Weight of 15,238 eggs.....	60 grams



The following data apply to the gonads of the male:

Average weight of 45 right testes.....	7.5 grams
Average weight of 45 left testes.....	6.5 grams
Total weight of gonads.....	14.0 grams

In every case the right testis exceeded the left in weight.

In order to ascertain the effect of temperature upon the fish, twenty-five ciscos were captured by means of a gill net and the ten least injured were brought in alive to the vivarium, where they were placed in a large concrete tank abundantly supplied with a constant supply of fresh running water. The fish lived well throughout the winter, with only an occasional mortality due to the fungus *Saprolegnia*. The water was kept at a temperature of 4.5°C during a period of four months, covering the breeding season. In spite of the fact that fifteen of the confined fish were females, all heavy with eggs, not a single egg was laid during this time. In a second tank, exactly similar to the first, and with the same water supply, but cooled by means of ice to a temperature of 3.5°C, females from the first tank spawned within ten minutes after transfer.

A second experiment consisted in transferring two females into the second tank while the water was at 4.5°C. After two hours in this tank, a large piece of ice was added and a careful record of the temperature kept. The first female spawned with the temperature at 3.6°C, the second at 3.4°C.

From the fact that the observed temperatures at which the fish spawn in nature coincide exactly with the observed experimental controls in the laboratory, namely 3.3° to 3.6°C, it must be concluded that these figures represent the critical breeding temperature of *Leucichthys artedi*. It must be further concluded that the temperature is the causal factor for egg deposition and that this critical temperature is needed before the eggs will be laid. This conclusion is inescapable as repeated oxygen and hydrogen-ion concentration determinations showed the conditions in the water to be almost constant for these factors, and the carbon dioxide variations were so very slight and in both directions that they must be considered as having no significance.

Nothing is known concerning the embryology of the species, and here again the writer has considered the subject as outside of his problem. However, it is well to point out that this egg is an ideal one for laboratory use and experimental purposes: it is easily obtainable, available for winter work, development is sufficiently slow for convenient study, and the egg is of fair size and remarkable clearness, having only a very few oil globules to obscure the cleavage. The writer has kept them in regulation egg-hatching glass jars until the embryo was well developed, when the set was accidentally destroyed by the breaking of the jar. These eggs were

fertilized in a glass dish at 3:30 o'clock in the afternoon of December 2, the fertilization membranes appearing around the eggs very quickly. At 9 P.M. the eggs were all in the 2-celled stage; at 12 midnight the 8-celled stage was nearly completed, while at 8 A.M. on December 3, the 64-celled stage was beautifully marked. The temperature here ran from 4.5°C to 5.5°C. At 3 o'clock that afternoon the cells were too numerous to count, and from then on the eggs were permitted to develop without observation. The exact length of the developmental period has never been worked out.

#### THE YOUNG

I believe that young ciscos are among the least known of all of the Wisconsin fishes. In fact, there is no evidence that anyone other than myself has ever taken them alive in nature, and it took me nine years of search before I finally got three individuals. These were young of the year, taken in Oconomowoc lake on July 20, 1922, in a trammel net set on the bottom in 52 feet of water. They measured 6.25 cm in length, and are the only young-of-the-year that I have ever handled. Much popular misinformation is in circulation in southern Wisconsin concerning the young cisco, as the brook silversides (*Labidesthes sicculus*) is uniformly considered as the young of *Leucichthys artedi*. This is due largely to a certain similarity of shape and color, and to the well known lack of discriminate observation on the part of people in general. This mistaken identity works for the good of the silversides, for as the cisco is protected by law, many bait gatherers scrupulously return *Labidesthes* to the water.

As the ice forms over the shallow water very soon after the eggs are laid, difficulties in determining the movement of the young after hatching are greatly increased. Upon hatching the young fish seek the deep water, and this occurs prior to the complete breaking up of the ice in the spring, which takes place usually about the first or second week of April. Repeatedly have I marked the spot where eggs were deposited, only to find them hatched when the breaking of the ice made re-examination possible. That the hatching takes place late in March is suggested by the condition of development of eggs retrieved by chopping through the ice in late February and early March. This would make the developmental period between ten and twelve weeks, probably with considerable variation depending upon the temperature conditions, longer during a long winter, and shorter in the case of an early spring. The young, then, seek the deep water where, because of their small size, they are almost entirely inaccessible for study. There is nothing to indicate that anything of unusual interest takes place during this juvenile condition.

Through the coöperation of the dozens of fishermen who catch the cisco through the ice during the winter, the writer has had the opportunity of examining hundreds of specimens for size measurements and food habits.

The results of these examinations are summarized in table 25 which shows age, length and weight measurements. This table gives the number of fish of different ages examined during the last week of January and the first week of February 1923 and 1924, together with their weight in grams and their length in centimeters. In compiling the table the sexes were not separated as the compilation was made nearly two months after the

TABLE 25

THE WEIGHT AND LENGTH OF CISCOS OF DIFFERENT AGES IN  
OCONOMOWOC AND PINE LAKES

Age Years	OCONOMOWOC LAKE			PINE LAKE		
	No. Fish Examined	Weight grams	Length cm	No. Fish Examined	Weight grams	Length cm
5 mos	3	22	6.2	—	—	—
2 yrs.	26	105	13.5	11	45.0	12.5
3	144	166	17.4	41	60.2	16.2
4	168	257	22.3	54	85.2	19.5
5	340	366	28.2	108	119.8	24.6
6	279	445	31.5	172	190.0	28.3
7	138	527	33.6	95	262.4	31.4
8	76	611	36.2	36	342.7	33.0
9	14	623	37.4	17	406.2	33.8
10	11	696	38.6	3	436.1	34.5

spawning period and hence the error inevitable in the case of ripe females is not introduced. Furthermore, growth curves for the sexes coincide so exactly that no conclusions can be drawn other than that the sexes develop at essentially the same rate.

The comparison between the cisco of Oconomowoc lake and that from Pine lake is exceedingly interesting, and the relationship is well brought out in figure 21, where the growth in grams has been plotted against the age in years of fish from the two lakes. Oconomowoc lake contains the type of cisco most commonly found in the southern Wisconsin lakes, while the Pine lake fish are on the average much smaller in size and weight than those of any other lake in the county, yet entirely typical of the species from a morphological and ecological point of view. Figure 22 shows the length in centimeters plotted against the age in years for the two lakes. From these figures it is seen that, while the fish do not differ greatly in their relative lengths at the different ages, their weights do not agree at all closely. An explanation of this condition is to be found in the physical factors involved. The cisco is more abundant in Pine lake than in any other lake in the county, probably many times more numerous. I have sat in a fish house on the ice during the winter and watched the fish through a



hole in the ice, and have been utterly astonished at their numbers: a thick mass of fish from just below the ice as far down as the eye could see. An examination of the water of Pine lake shows that the plankton organisms are relatively less abundant per liter of water than in Oconomowoc lake. Thus one can explain the weight discrepancy on the basis of inadequate food supply: there are too many fish for the amount of food available. A similar condition is to be found in Otis lake in the case of the large mouthed black bass (*Micropterus salmoides*) this is a small lake to which the public does not have access, and it is full of bass, many times more than the food will suffice for anything over a strict maintenance ration. The result is a large number of bass of light weight and scanty measurements. In a similar way one occasionally catches a cisco in Pine lake that weighs over a pound and still is but five or six years old; but such a one must be looked upon as a particularly fortunate individual in so far as food supply is concerned.

#### FOOD HABITS

The cisco is one of the most exclusive plankton eaters among our fishes. The food of the immature fish—up to about 16 cm. in length—is 100% plankton organisms, being composed of Cyclops, Daphnia, Diaptomus, Bosmina, Chydorus, rotifers and other animals of a similar nature. Bottom material is freely taken into the alimentary canal and as this contains a considerable amount of vegetable matter, the smaller algae, diatoms etc. form a part of the diet. As the fish reach a larger size the food assumes a wider range, and various mollusks, insect larvae, crustacea and small fish appear in the food list. There is a slight tendency on the part of the fish to feed more upon the micro-crustacea of the Daphnia-Cyclops type during the winter than during the summer, but in Oconomowoc lake, as in all of the lakes in Waukesha county which the writer has investigated, these organisms form normally a large part of the diet the year around. This is at variance with findings of Pearse (1921a) in the case of *Leucichthys birgei* in Green lake in summer, where he found 61.2% of the food to be amphipods. However, his numbers are hardly large enough to base conclusions upon, nor is the seasonal range of his investigations of sufficient duration: he had but 30 fish caught between August 13 and 19. In table 26 the writer presents a summary of 941 stomach examinations grouped according to months in sets of two months to a group. In this table the Cladocera are represented by species of Bosmina, Daphnia and Chydorus; the Copepoda by Diaptomus and Cyclops; the Ostracoda by Cypris. The mollusks include various species of Amnicola, Valvata, Sphaerium, Pisidium and Planorbis. Sayornis (formerly Corethra) has been separated from the other insect food because of its abundance and frequency. The heading "other insects" includes various larvae and pupae picked up from

the bottom, largely Ephemera and Plecoptera, Chironomus and an assortment of adult insects picked up off the surface during the summer when the fish occasionally come to the surface on a quiet evening. The fishes eaten are usually in such a state of digestion that identification was

TABLE 26  
THE PERCENTAGE OF VARIOUS ITEMS OF FOOD OF THE CISCO  
THROUGHOUT THE YEAR IN OCONOMOWOC LAKE

Month Number	Jan. 482	Feb. 26	Mar. 26	Apr. 91	May 140	June 140	July 128	Aug. 128	Sept. 64	Oct. 64	Nov. 64	Dec.
Food												
Ostracoda	1.5		0.5		1.9		2.3		3.5		1.0	
Copepoda	26.5		17.6		20.3		13.3		19.8		15.4	
Cladocera	30.7		22.8		24.1		20.8		24.6		18.6	
Amphipoda	4.5		3.9		1.0		1.2		3.1		5.8	
Mollusca	8.1		7.4		2.6		3.2		1.9		2.4	
Sayornis	13.5		23.8		18.8		20.1		25.6		19.8	
Other Insects	4.3		12.6		9.4		6.8		9.2		8.6	
Fishes	2.2		3.4		2.6		7.1		2.1		3.9	
Vegetation	2.9		2.6		6.3		3.0		4.5		9.4	
Inorganic	3.8		4.2		8.1		3.4		3.4		6.5	
Miscellaneous	2.0		1.2		3.6		2.3		2.3		9.6	

utterly impossible, but scales found in the stomach has hinted that these are often young of the cisco itself. The vegetable matter includes algae and plant debris from the bottom. The inorganic matter is largely fine silt or sand, taken in as the fishes nose around on the bottom. The miscellaneous item includes forms not found in any great numbers, such as water mites, rotifers (Anuraea) and unidentifiable matter.

Certain facts in connection with the food habits deserve mention. During the winter months it is a common occurrence to find a stomach simply packed with entomostraca. One such stomach, from a fish 31 cm long and weighing 446 grams, was carefully washed out and the contents preserved in alcohol. This mass was then diluted in 250 cc of alcohol and five samples of 2 cc each were carefully counted on a squared plate. The average of the five counts gave the following:

Daphnia . . . . . 541; in 250 cc. . . . . 67,625  
Cyclops . . . . . 263; in 250 cc. . . . . 32,875  
Bosmina . . . . . 121; in 250 cc. . . . . 15,125

Total: . . . . . 115,625

This gives some idea of the tremendous numbers of organisms these fish consume. A stomach was found in January, 1924, which contained nothing

except *Sayomia albipes* larvae. By actual count 376 larvae were obtained, of which 319 were still alive when removed from the stomach after the fish had been out of water over three hours. While *Sayomia* forms a very stable article of diet, the larvae seem to be more resistant to the digestive juices of the cisco than any food consumed, as in a vast majority of the stomachs examined the larvae have shown great activity after removal, a condition found in no other item of food eaten by the fish.

#### MIGRATIONS

It has been said that the cisco is a bottom inhabitant and that it must be regarded as a deep water fish. During that part of the year when the oxygen conditions permit, *Leucichthys artedii* remains normally in the deep water, spending most of the time within a meter or two of the bottom. This fact has been demonstrated again and again, year after year by the use of gill nets set at different depths. As I have said, this differs radically from the habitat chosen by the Lake Michigan cisco as reported by Ward (1897). However, with the formation of the thermocline and the accompanying increase in the area of water deficient in oxygen, the cisco is forced to leave the bottom waters of the deeper parts of the lake, and assume a position ever higher in a vertical scale. As the thermocline climbs upward the cisco comes up with it and assumes a position in relation to the thermocline which may be described as directly above it. Therefore, if one takes the temperature of the water at different depths and thus obtains a fairly accurate idea of the location of the thermocline, one can set gill nets just above this depth and catch ciscos all summer. This was discovered in 1916 when the writer wanted the fish for an examination of the summer food. Nets were set in the deep water where the fish were caught in abundance during the previous winter, and caught nothing. After repeated failures a series of eight nets was set, one above the other. The net which was at 10 meters yielded 11 ciscos; the one at 9 yielded none and the one at 11 yielded 2 in the upper foot of mesh; none was caught in any other net. An analysis of the water at that time showed that the thermocline stood at 11 meters. This idea has been followed ever since, and has always yielded fish. I have set 43 nets below the thermocline, in 9 different lakes, and have never in a single instance caught a cisco. From these facts one must conclude that, while the cisco is essentially a deep water fish, it is driven from its chosen habitat by uncongenial gas conditions, so that the species really has a seasonal migratory rhythm in a vertical plane, correlated with and determined by the shifting of the thermocline.

This action of the thermocline in forcing the cisco up from the bottom has an exceedingly important effect upon the fish concerned. Being an inhabitant of the deep water, it is a cold water species. (Fig. 23.) The early summer influence of the thermocline has little effect on the cisco as



there is still a great abundance of cold water rich in oxygen, but every meter, every centimeter that the oxygen level creeps upward, the amount of cold, oxygen-abundant water is cut down, and the fish is forced into water of increasing warmth. In the case of very hot summers, when the thermocline ascends unusually high, the cisco is forced into water far warmer than that which it ordinarily selects and to which it is therefore best adapted. The result is often disastrous. Dead fish begin to appear floating on the surface, fish perfect in every detail, unscarred, unparasitized, uninjured. Dozens of the fish I have picked up just as they reached the surface, to find them still alive though barely active. If the wind is blowing the shores of certain lakes, particularly Pine, Okauchee and Oconomowoc, become lined with dead fish. I was called to investigate such an "epidemic" among the cisco of Pine lake in August 1917. On the west (windward) shore I counted 72 dead fish in less than 100 feet of shore line, and this was by no means exceptional. As the result of my survey at that time I estimated that no less than 175,000 ciscos died within a week in that lake alone. This is significant when one considers what I have already said about the abundance of the fish in the lake. Similar catastrophes have occurred in Oconomowoc, La Bella, Okauchee and Silver lakes, though in no other lakes have the numbers run so high. Okauchee lake has come the closest to the record set by Pine and it ranks second in the abundance of the species in its waters. It is significant to note, also, that it is the larger fish which are most affected, suggesting a greater adaptability, resistance and vitality on the part of the young fish. It is further to be noted that the mortality is highest among the females which at this season of the year already have a considerable mass of spawn in the body, and this may explain the excess of males over females to which I have already alluded. There is no remedy for these "epidemics": they are caused by the fish being forced into the warm upper stratum of water by the rise in the thermocline, and the fishes are simply not physiologically adapted to warm water conditions. For the purpose of determining the effect of temperature upon *Leucichthys artedi*, several fish were placed in a large tank on February 3, 1924. The temperature of the water was noted, as were the gas conditions, and then warm water from a boiler was permitted to enter the tank slowly at one end. The results are shown in figure 16. Here it will be seen that the fish avoid water above 17°C if possible, but will stand a temperature of several degrees above this. At 26°C they begin to float at the surface; this is very close to the temperature encountered in nature after a prolonged, quiet, hot spell of a hot summer. The pH readings throughout the experiment showed no indication that the hydrogen-ion concentration was concerned with the reaction of the fishes; the same was true for oxygen. Since the fish require more oxygen with a rise in the temperature of the water, the amount varying

directly with the increase in temperature, one can explain the mortality as being due to three factors: 1) the thermocline; 2) warm water; and 3) insufficient oxygen available. The thermocline is responsible for the situation. (Figs. 6, 7.)

A second migratory rhythm was discovered when it was found that the fish in Oconomowoc lake under ordinary conditions were nearer the surface at night than during the day. That this is not a phototropic reaction is indicated by the fact that they can easily be attracted to the surface during the hours of daylight, and that they will remain under the ice during the winter for hours at a time under the brightest of light conditions, if food is available. This suggested the idea that this daily movement might be a feeding rhythm. Since the fish were found to be feeding entirely upon entomostraca at the time (February 2) a series of water samples was taken at different depths at noon and again at the same depths at midnight. The four chief organisms found were *Daphnia*, *Cyclops*, *Diaptomus* and *Bosmina*. The water was pumped up by means of a garden hose and was strained through the Birge and Juday plankton catcher kindly loaned me by Mr. Juday. The amount of water strained was 15 liters from each depth. Figure 24 shows the distribution of these four organisms at the different depths during the day and at night. It will be noted that in every case the organisms migrate upward at night, the amount of the vertical change being the least in the case of *Cyclops* and greatest in *Daphnia* and *Diaptomus*. Since the cisco is dependent upon these organisms for food, and since it is well known that these minute entomostraca have such a daily rhythm, and, lastly, since the water conditions are uniform in the winter and the fish show no suggestion of negative phototropism, it must be concluded that this daily movement is a feeding rhythm following that of the entomostraca. Repeated observations and examinations have borne out this conclusion.

#### BEHAVIOR

I have stated in the discussion of *Labidesthes sicculus* that, were it not for the fact that the silversides lie quiescent during the dark nights it would be the most active of all our fishes. But this title belongs to the cisco which is active, apparently, from the time it hatches until it dies. I have had the cisco under observation in the laboratory for nine months; I have spent two weeks each winter for nearly twelve years watching the behavior of the fish through the ice and I have never yet seen one quiet for a period even approaching a second. This constant activity is perhaps due in a large measure to the food habits of the fish; since their chief item of diet is entomostraca and since these are eaten in enormously large numbers as has been shown, it follows that great quantities of water must be passed through the gill rakers in order to obtain this food in quantities such as

are found in the stomach. A cisco with an empty stomach is the greatest rarity I recall in the fish life of the region under consideration, rarer even than young of the species, for I have yet to find a single empty stomach in a healthy fish.

That the species is gregarious is borne out by the fact that during the winter when the fish are sometimes seen at the surface, neither I nor any of the hundreds of cisco fishers with whom I have spoken have ever seen a lone cisco. When traveling near the surface at times the schools are seen to number several hundred individuals; the smaller schools are composed of from twenty to sixty fish. While these schools are to a certain extent composed of fish of varying sizes, the large and small fish do not mingle to any great degree, there being a marked uniformity of size in the component individuals in each school. That these facts hold also for the summer months is indicated by the gill net catches. Often I have missed a catch entirely, but the smallest number of fish I ever caught is 5; the largest is 33, in a fifty foot net, four feet deep with one and one half inch mesh. Surely this shows unmistakable gregariousness.

During the summer when the thermocline has driven the fish from the deepest water, the fish travel in schools, paralleling exactly the contours of the sand bars. The interesting fact about this travel is that it has a definite direction: the fish travel west along the north shore of Oconomowoc lake, south along the west shore, east along the south shore and north along the east end of the lake. This has been demonstrated by noting the direction in which the fish are found in the gill nets along the different shores. This is brought out in table 27.

TABLE 27  
THE DIRECTION OF TRAVEL OF THE CISCO ALONG THE SHORES OF  
OCONOMOWOC LAKE IN SUMMER

Shore	Net set	No. caught	N	Number heading		
				S	E	W
North	E-W	286	1	3	—	—
North	N-S	4	—	—	12	276
West	E-W	83	4	79	—	—
West	N-S	0	—	—	—	—
South	E-W	6	4	2	—	—
South	N-S	146	—	—	133	13
East	E-W	74	59	15	—	—
East	N-S	10	4	6	—	—

These figures are the result of a series of catches during the summers of 1921 and 1922 and represent the total catch of 20 nets set in each direction along the shore. The low figures for the east and west shores are explainable



by the fact that the bars are much less regular here than along the north and south shores, and the schools go south at the west end and north at the east end over a scattered territory. The figures show conclusively that the line of travel is well laid down. There is at present no explanation for the phenomenon; there is no evidence of oxygen, carbon dioxide, hydrogen-ion concentration, light or temperature changes to account for it, nor can it be a reaction to current, for down the north shore the fish are following the current caused by the incoming Oconomowoc river, while along the west and south shores they are going against the current caused by the outflow of the Oconomowoc river at the northwest corner of the lake. It is difficult to see in what way it could be linked to the food habits, for certainly the entomostraca have no such migratory movement.

However, that the movement of the fish is intimately connected with their food habits is indicated by the fact that a migrating school can be stopped by an abundant food supply. This fact is well known to the winter fishermen who utilize it to their benefit by dropping oatmeal flakes into the water. Upon the descending flakes and the accompanying dust the fish feed ravenously, and a series of schools can be held under the holes in the ice for weeks at a time while hundreds of fish are caught from the schools by means of a small "white bait" or a gold bead. Once the school has been stopped in this way, the stomachs show nothing but oatmeal—the normal food habits are entirely abandoned. Any small object descending slowly through the water is taken into the mouth, but if it be not satisfactory it is ejected again with astonishing rapidity. This oatmeal diet is not injurious to the fish, though the flesh is noticeably softer after the fish have been feeding upon it for some weeks. A few years ago meat scrap was used instead of oatmeal; it was eaten even more ravenously than the meal, but resulted in diarrhea and in the death of many fish, so that its use had to be prevented by law. (Fig. 5.)

One further point should be noted in this connection. In the lakes of the north, where lumbering causes a constant distribution of sawdust over the water, the writer has found dead *Leucichthys* floating at the surface, with stomachs containing a solid mass of sawdust. These descending particles are no doubt taken in with the water, strained out by the gill rakers, mass in the stomach and eventually kill the fish which is unable to void the debris.

#### CONSERVATION

It is generally said that the cisco will bite only during the winter, but this is not correct as the writer has often proven. Still no one fishes for them in the summer, which is just as well. Cisco fishing has been a winter sport in the county for forty years and the catches are astonishing. No less, certainly, than 15,000 are taken from Oconomowoc lake each winter,

and this is repeated in other cisco inhabited lakes. In former years the catches were much larger, 200 fine fish a day per fisherman being a fair catch. A conservative estimate places the cisco catch in Oconomowoc lake during the last 40 years at least as high as 1,000,000 fish! There has been no restocking, for the cisco is not raised in any hatchery in the state. In spite of the fact that the species is prolific, the fact remains that the rate of growth is slow. The result of the enormous catch each year is that the size of the fish has been reduced about four fifths! I have a record of thirteen fish caught on March 3, 1908, that weighed over  $4\frac{1}{2}$  pounds each; a 3 pound cisco is still occasionally caught, but is very, very rare; dead fish are sometimes found during the summer that weigh upward of 4 pounds. But in the winter of 1924 the average weight of 244 fish weighed by the writer was just 116 grams—a little better than four to the pound!

Until the last few years there were no laws relating to the capture of the cisco in the inland waters of Wisconsin. Repeated pressure on the state legislature finally placed a bag limit of 25 per man each day on the species. But this is not sufficient. In view of the situation as it now stands the writer recommends the following conservation methods, these being well worth while as the species is a most excellent table fish.

1. Cisco fishing in all lakes in Waukesha county should be closed for a period of five years.
2. A size limit of 12 inches should be established.
3. The bag limit should be reduced to 15 each day.
4. The cisco should be raised in the bass hatcheries during the winter when these hatcheries are idle, and fry should be planted in suitable lakes.

#### SUMMARY

1. The cisco, *Leucichthys artedii*, is a member of the family Salmonidae and has a wide range in the deeper glacial lakes of the Mississippi valley, particularly in the northern part. It is known to occur in fourteen lakes in Waukesha county.

2. It is a deep water species, inhabiting the deepest parts of the lake during the winter, spring and fall.

3. Spawning occurs in late November or early December, the determining factor being the temperature of the water.

4. The males precede the females into the shallows, arriving when the water cools to  $4.3^{\circ}\text{C}$ . The females arrive a few days later, with the temperature dropping to  $3.8^{\circ}\text{C}$ , and spawning is at its height at  $3.3^{\circ}\text{C}$ .

5. Males outnumber the females, there being a higher mortality among the females during the warm water period of summer.

6. The eggs develop in from ten to twelve weeks, depending on the temperature of the water.

7. After hatching the young fish seek the deepest parts of the lake where they remain until their first breeding season, at the age of three years, except when driven out by the thermocline.

8. The rate of growth and weight increase is given for fish up to ten years of age.

9. The cisco has a seasonal migration in a vertical plane. This is due to the formation of the thermocline and the accompanying zone of water deficient in oxygen. The result is that the species is slowly driven from the deeper water into water of lesser depth and increasing warmth.

10. Since the cisco is a deep water fish, adapted to cold water, the result of this condition is death to thousands of fish. Death is due to suffocation as the fish require more oxygen in warm water than in cold, and the supply is insufficient to their needs.

11. The result of 941 stomach examinations is given, showing the food habits the year around.

12. Entomostraca form a very important item of the food. Since these organisms are negatively phototropic, being down during the day and up at night, a second migration, or daily rhythm on the part of the fish, also in a vertical plane, coincides with the movement of their food.

13. The fish are active day and night the year around.

14. This activity in summer assumes a definite co-ordinated movement, extending around Oconomowoc lake in a clockwise direction.

15. This movement is connected with the feeding habits as suggested by the fact that the migrating schools can be stopped and held by the presence of an abundant food supply.

16. The decrease in abundance and size of the cisco in Oconomowoc lake call for protective and conservative measures to prevent the destruction of a valuable food fish.



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#### EXPLANATION OF PLATES

The following photographs are from original negatives made by the writer within the limits of Waukesha county, Wisconsin. The graphs and diagrams are made from original data taken both in Waukesha county and at Madison, Wisconsin, the data being included in the body of the paper..

## PLATE I



## EXPLANATION OF PLATE I

FIG. 1. Laura Lake. A small body of water showing signs of old age.

FIG. 2. Pretty Lake. A small body of water that is nearly completely filled up. The mound in the middle foreground formerly was an island.







## PLATE II

## EXPLANATION OF PLATE II

FIG. 3. The Cisco, *Leucichthys artedi*, from Oconomowoc Lake.







## PLATE III

## EXPLANATION OF PLATE III

- FIG. 4. The zone of wave action along a steep shore, marked by a paucity of vegetation and fish life.
- FIG. 5. Shanties used by cisco fishermen in Waukesha county during the winter fishing season. Oconomowoc Lake.







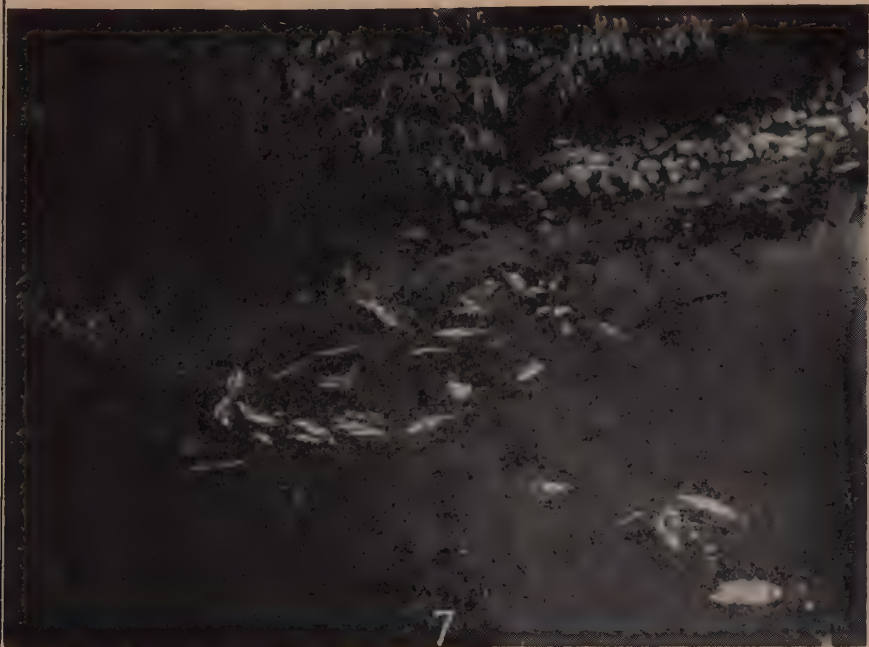
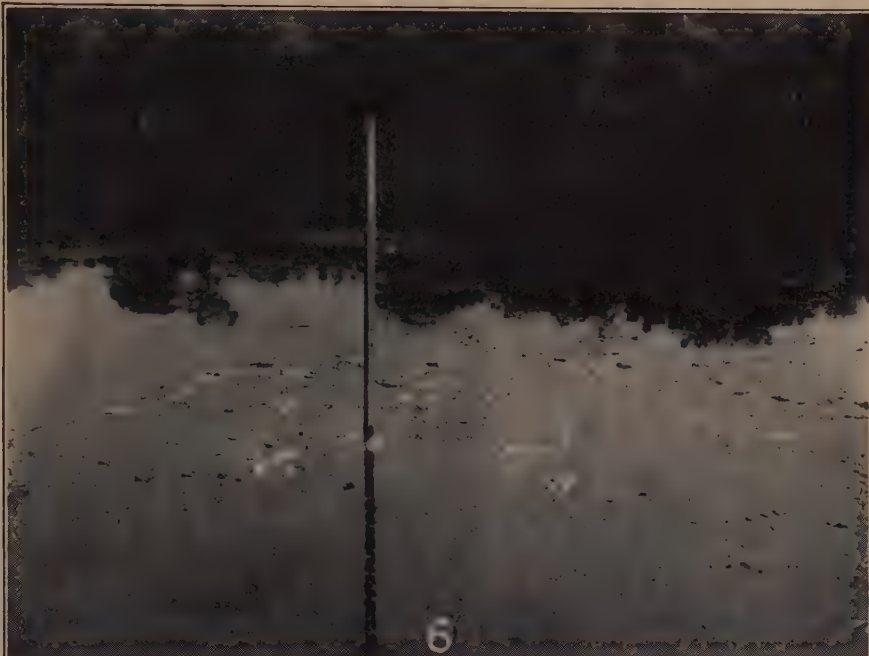
## PLATE IV

## EXPLANATION OF PLATE IV

FIG. 6. Forty-eight dead ciscos along fifteen feet of shore. Okauchee lake epidemic of August, 1925.

FIG. 7. Fifty-six dead ciscos drifting into shore during the Okauchee lake epidemic of August, 1925.





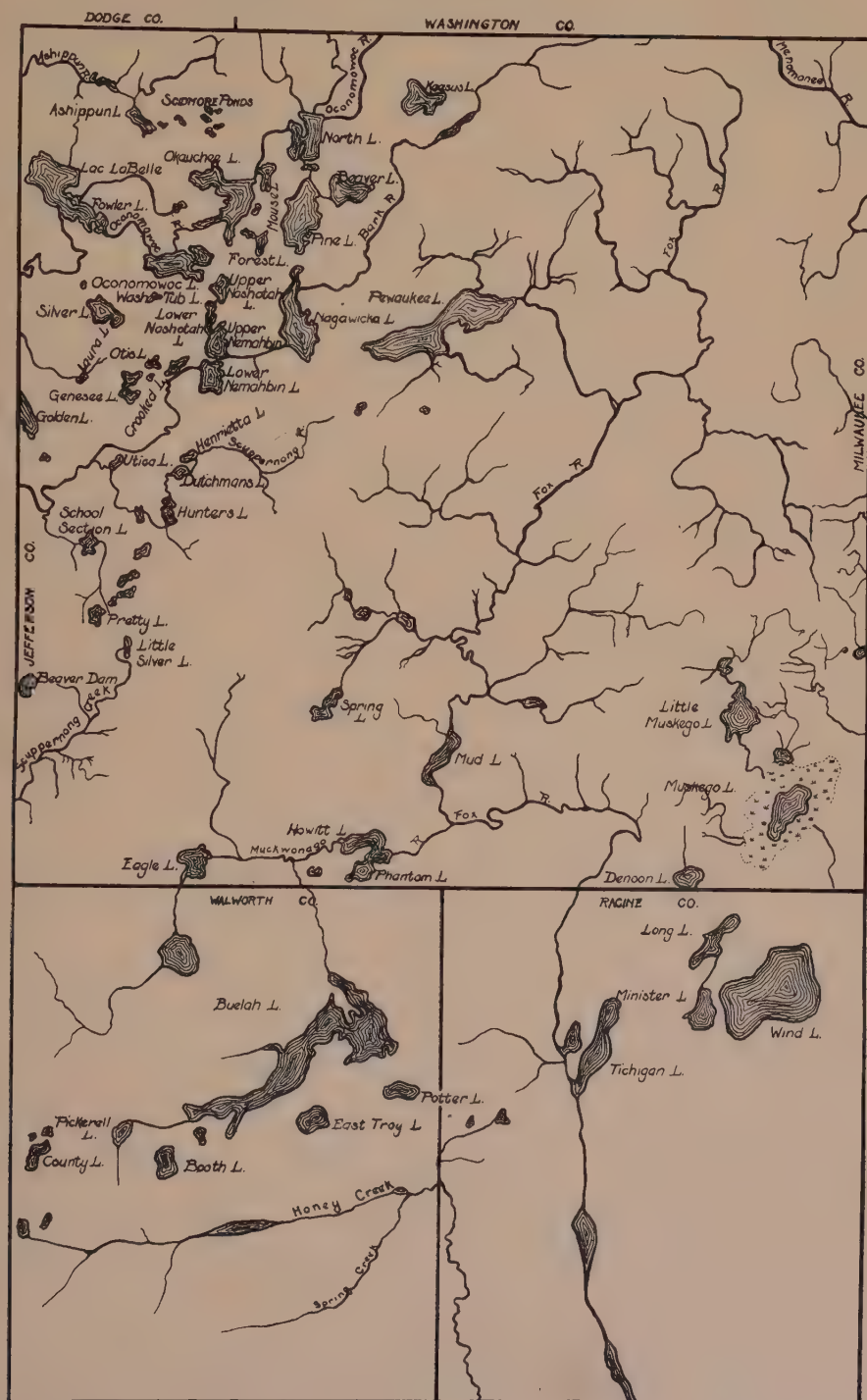


## PLATE V

## EXPLANATION OF PLATE V

FIG. 8. Sketch map of Waukesha county, Wisconsin, and the region joining it to the south, showing the distribution of the lakes and river systems.





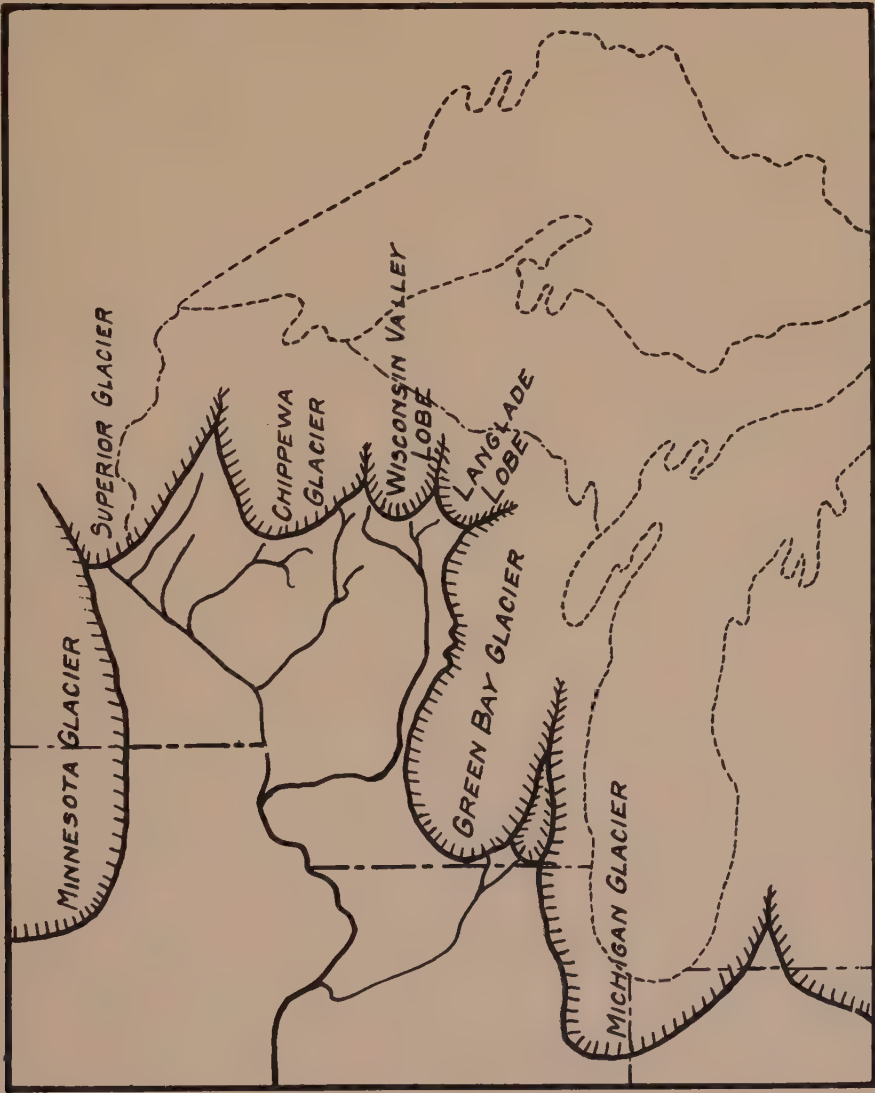


## PLATE VI

## EXPLANATION OF PLATE VI

FIG. 9. The Labrador glacier and its principal lobes. It is this ice sheet which is responsible for the outstanding topographic features of Waukesha county. (Modified after Fenneman)





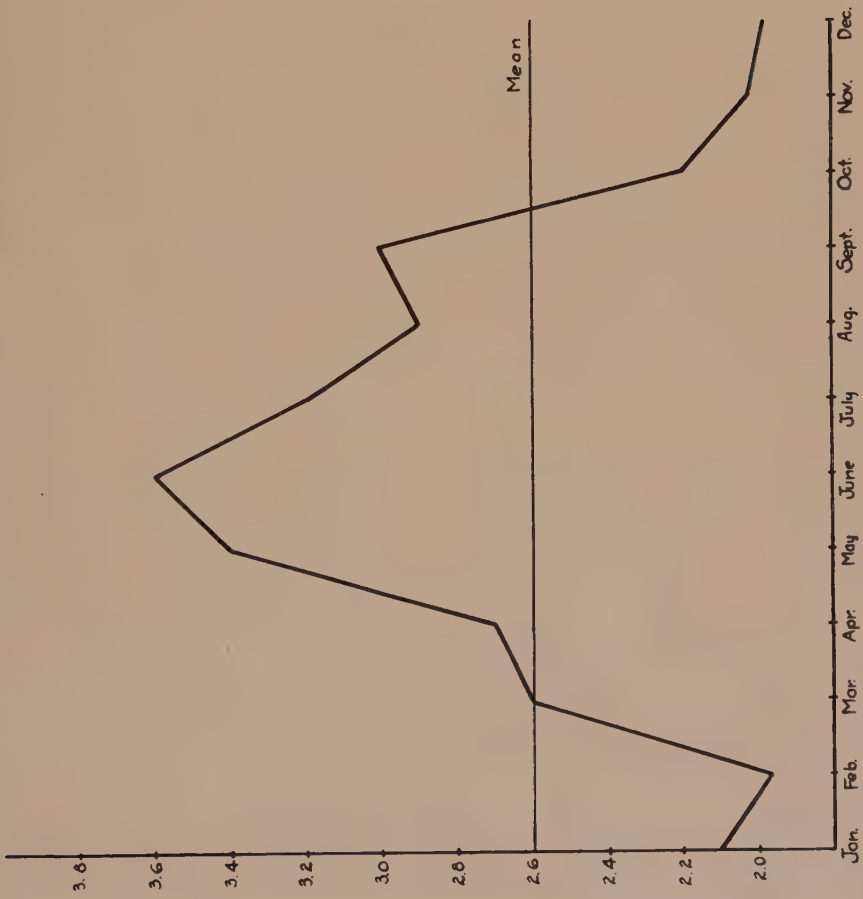


## PLATE VII

## EXPLANATION OF PLATE VII

FIG. 10. Graph showing the mean rainfall in inches per month in Waukesha county, Wisconsin from 1871 to 1924 inclusive. Station located in city of Waukesha.





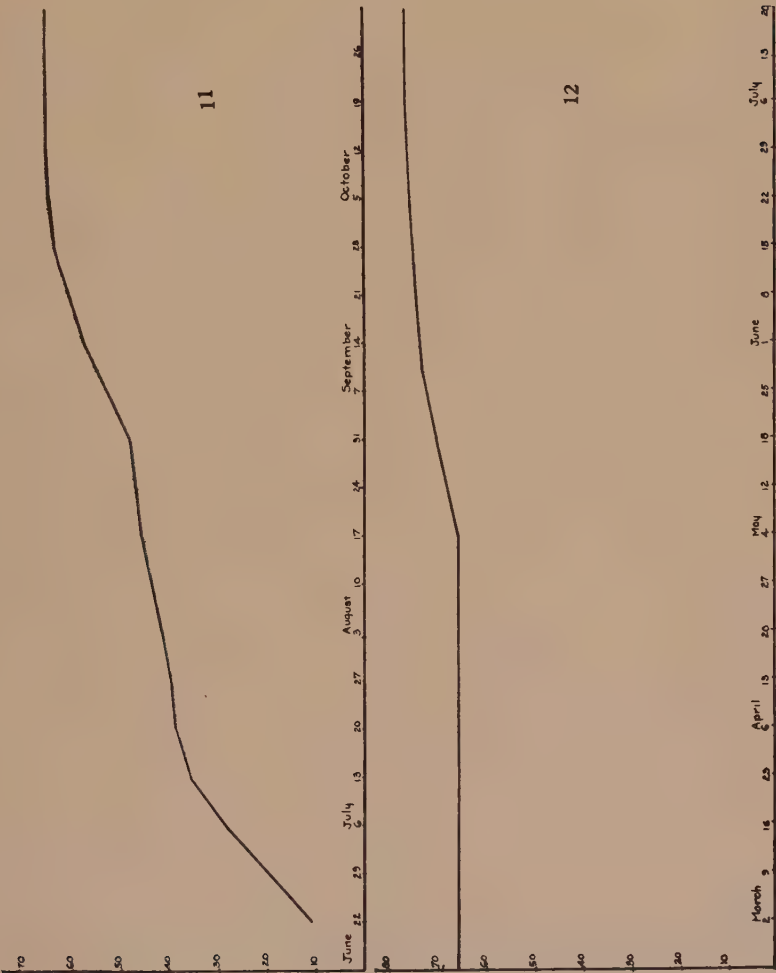


## PLATE VIII

## EXPLANATION OF PLATE VIII

- FIG. 11. Growth curve for brook silversides, *Labidesthes sicculus*: June to November. Length in millimeters.
- FIG. 12. Growth curve for brook silversides, *Labidesthes sicculus*: March to August. Length in millimeters.





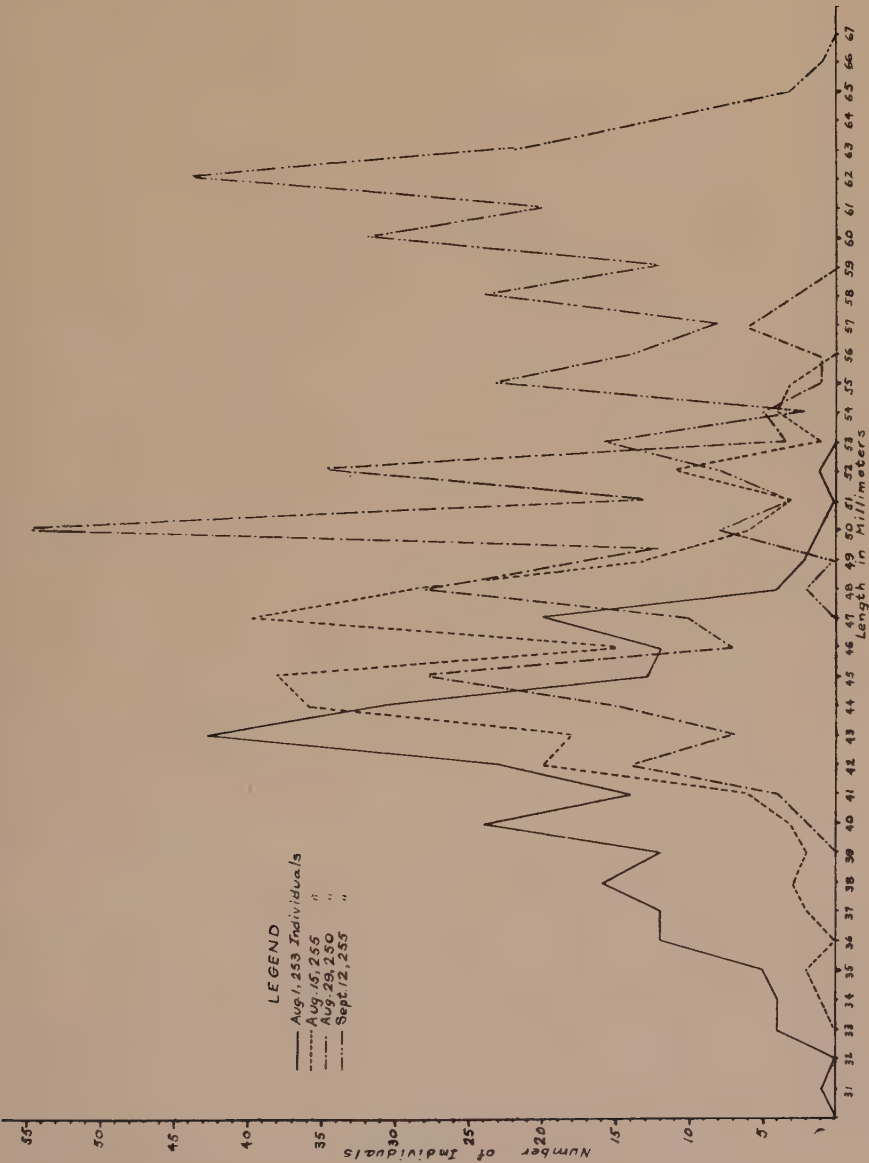


## PLATE IX

## EXPLANATION OF PLATE IX

FIG. 13. Measurements of 250 young-of-the-year of the brook silversides, *Labidesthes sicculus*, on different dates during the summer. Length in millimeters. Data from north shore of Oconomowoc lake.







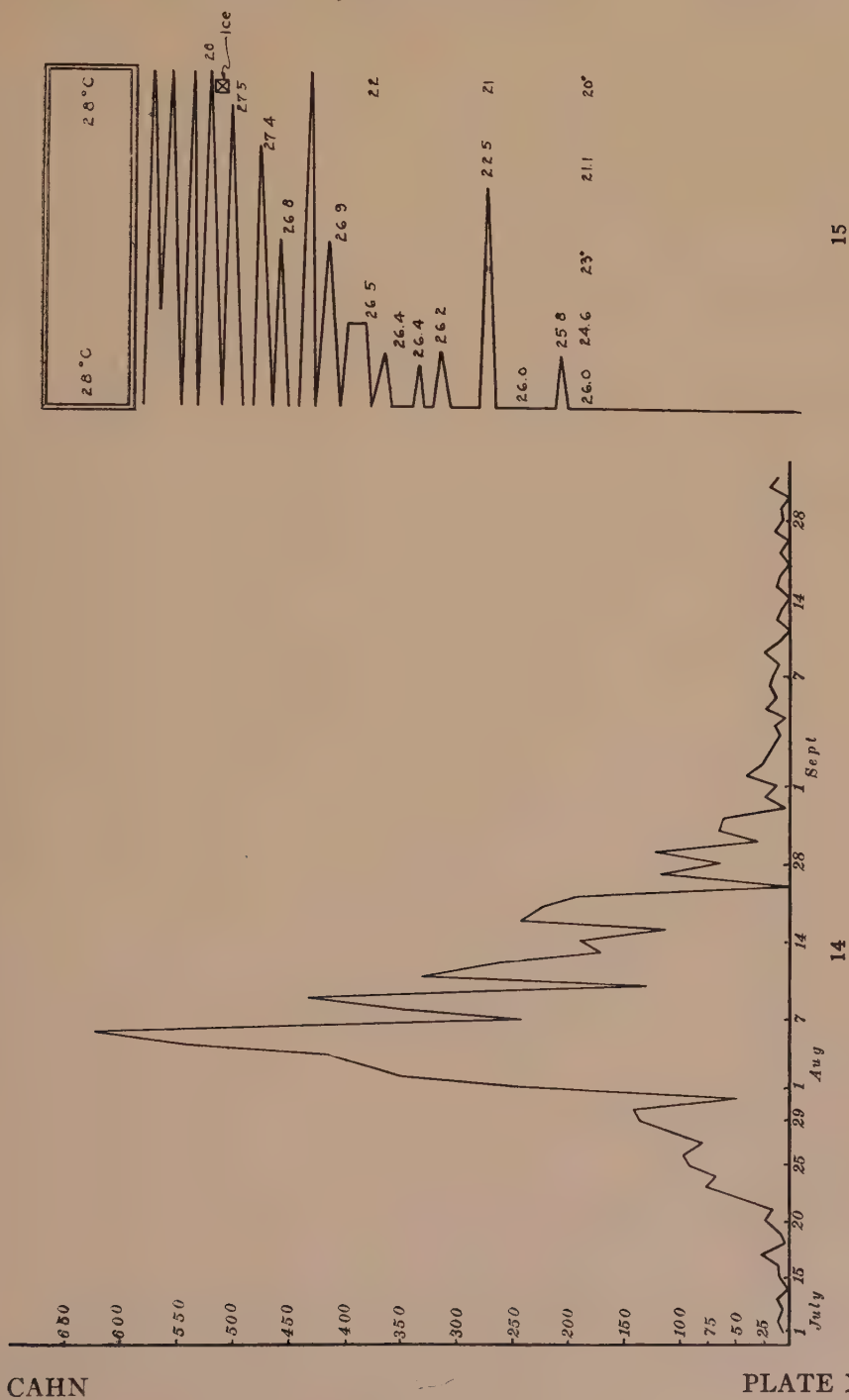
## PLATE X

## EXPLANATION OF PLATE X

FIG. 14. Showing the abundance of the brook silversides at night along the north shore of Oconomowoc lake, July 10 to Oct. 5, 1923.

FIG. 15. Figure to show the reaction of the brook silversides to water of increasing coldness.







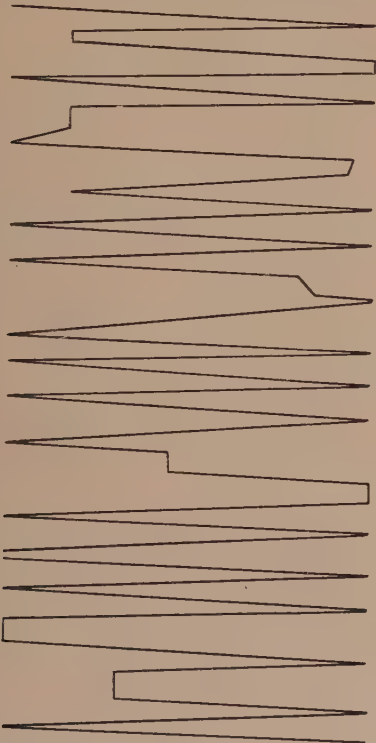
## PLATE XI

## EXPLANATION OF PLATE XI

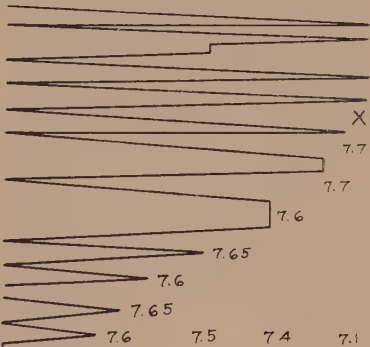
FIG. 16. Showing the reaction of the brook silversides to objects of large size.

FIG. 17. Showing the reaction of the brook silversides to water of increasing acidity.





16



X Acid

7.7

7.7

7.6

7.65

7.6

7.65

7.6

7.5

7.4

7.1

7.5

7.5

7.4

7.2

6.8

7.4

7.1

6.8

17

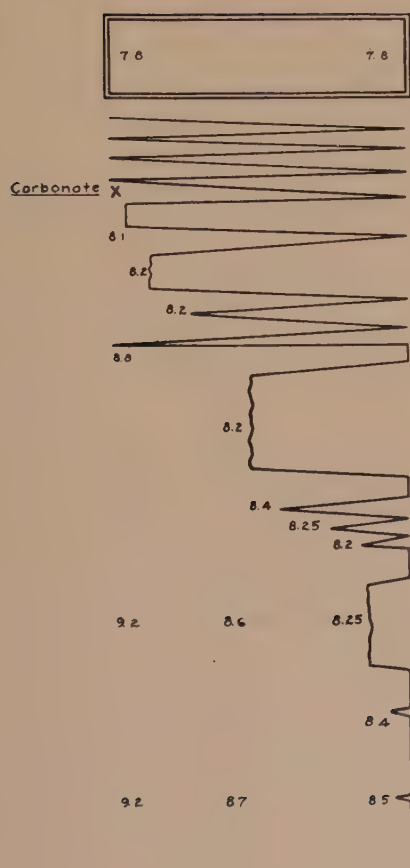


## PLATE XII

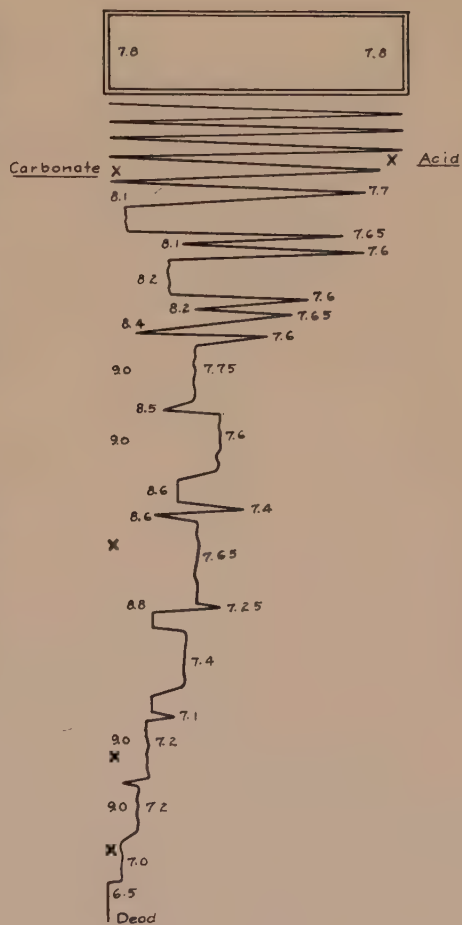
## EXPLANATION OF PLATE XII

- FIG. 18. Showing the reaction of the brook silversides to water of increasing alkalinity.  
FIG. 19. Showing the reaction of the brook silversides to water of increasing acidity and alkalinity.





18



19

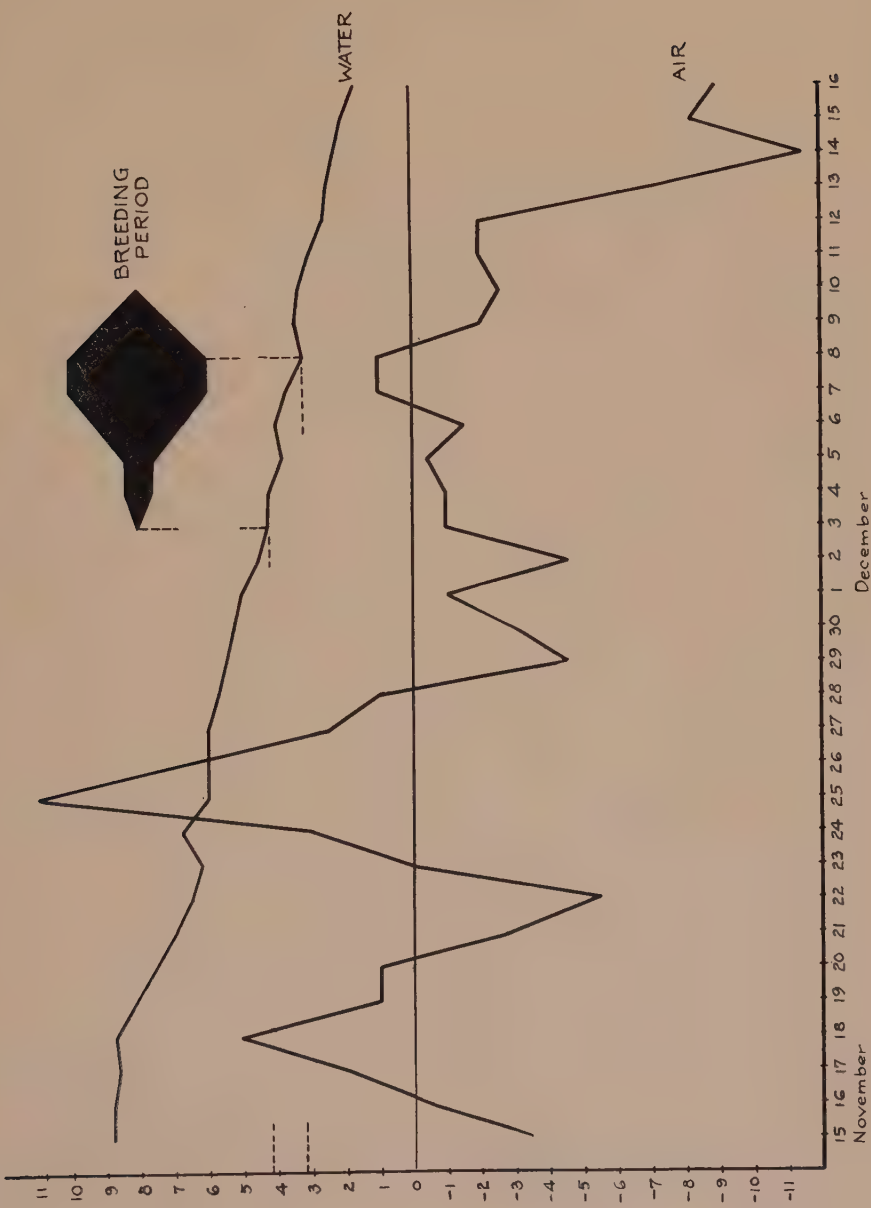


## PLATE XIII

## EXPLANATION OF PLATE XIII

FIG. 20. Showing the spawning period of the cisco in relation to the temperature of the water and of the air. Data from Lake Mendota at Madison, Wisconsin, Nov. 15 to Dec. 16, 1916. This is typical of the conditions existing during the spawning period in the Waukesha county lakes.





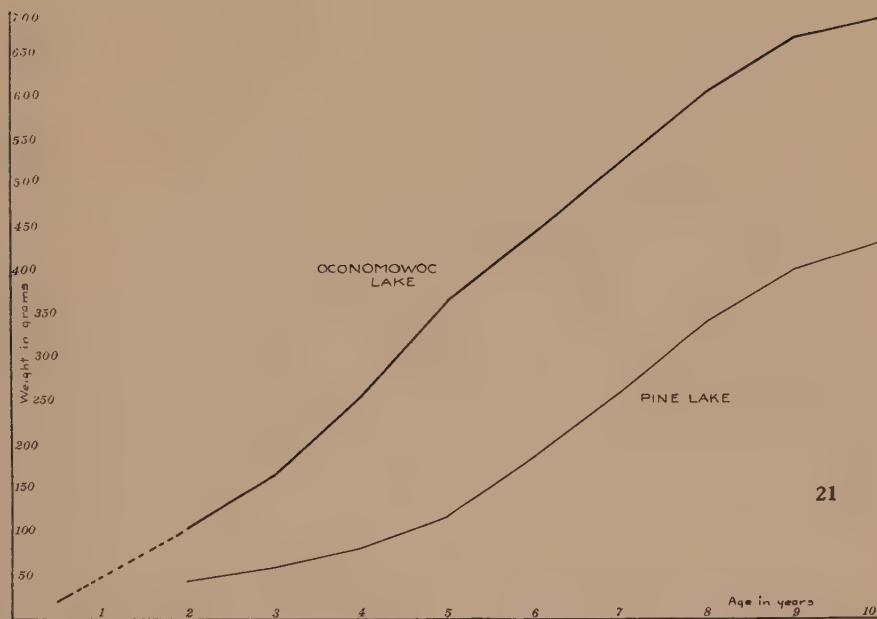


## PLATE XIV

## EXPLANATION OF PLATE XIV

- FIG. 21. Showing the relationship existing between ciscos from Pine and Oconomowoc lakes. The age in years is plotted against the weight in grams. Pine lake has many times more ciscos per volume than has Oconomowoc lake.
- FIG. 22. Showing the relationship existing between ciscos from Pine and Oconomowoc lakes. The age in years is plotted against the length in centimeters.





21



22

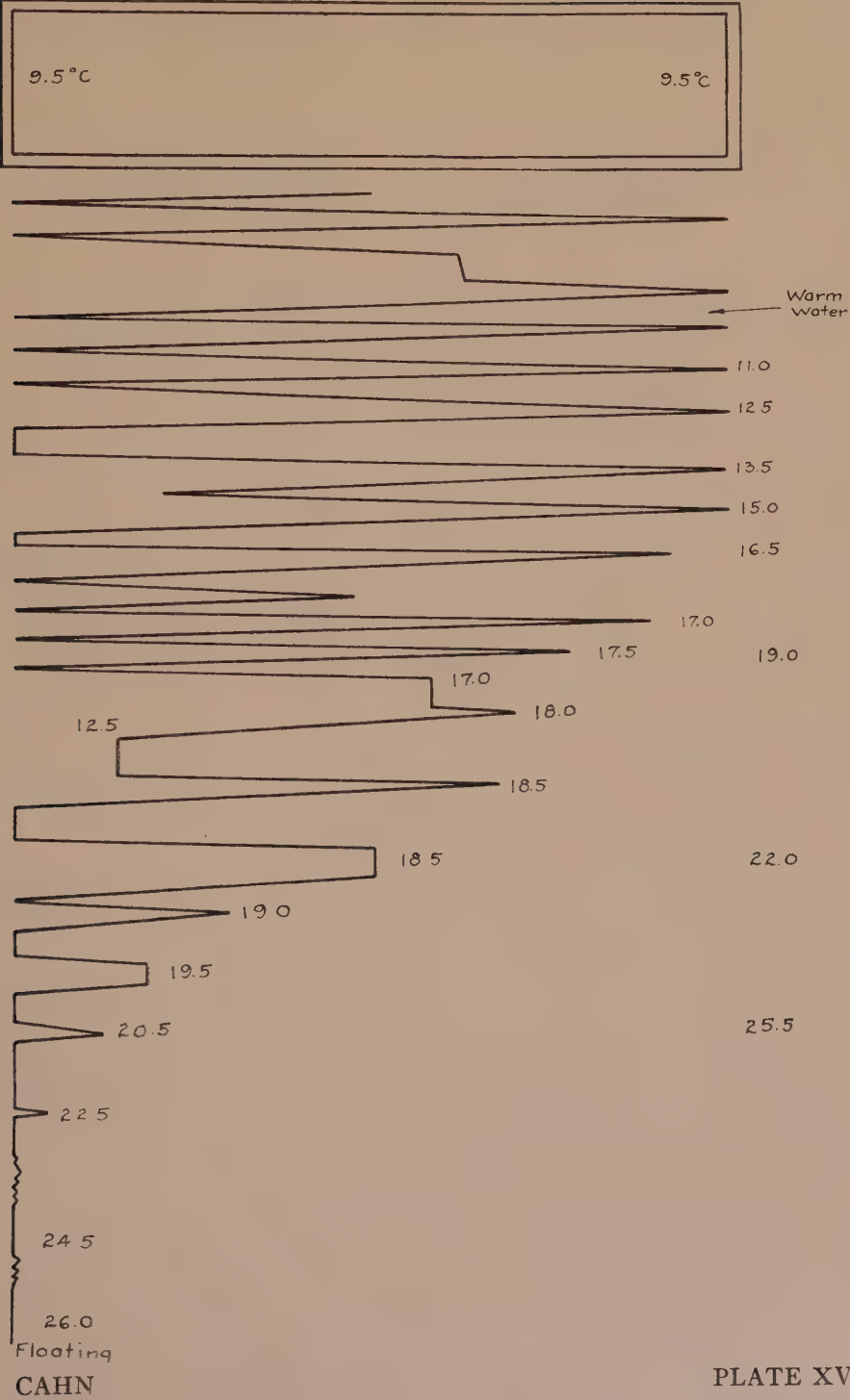


## PLATE XV

## EXPLANATION OF PLATE XV

FIG. 23. Showing the reaction of the cisco to water of increasing temperature.



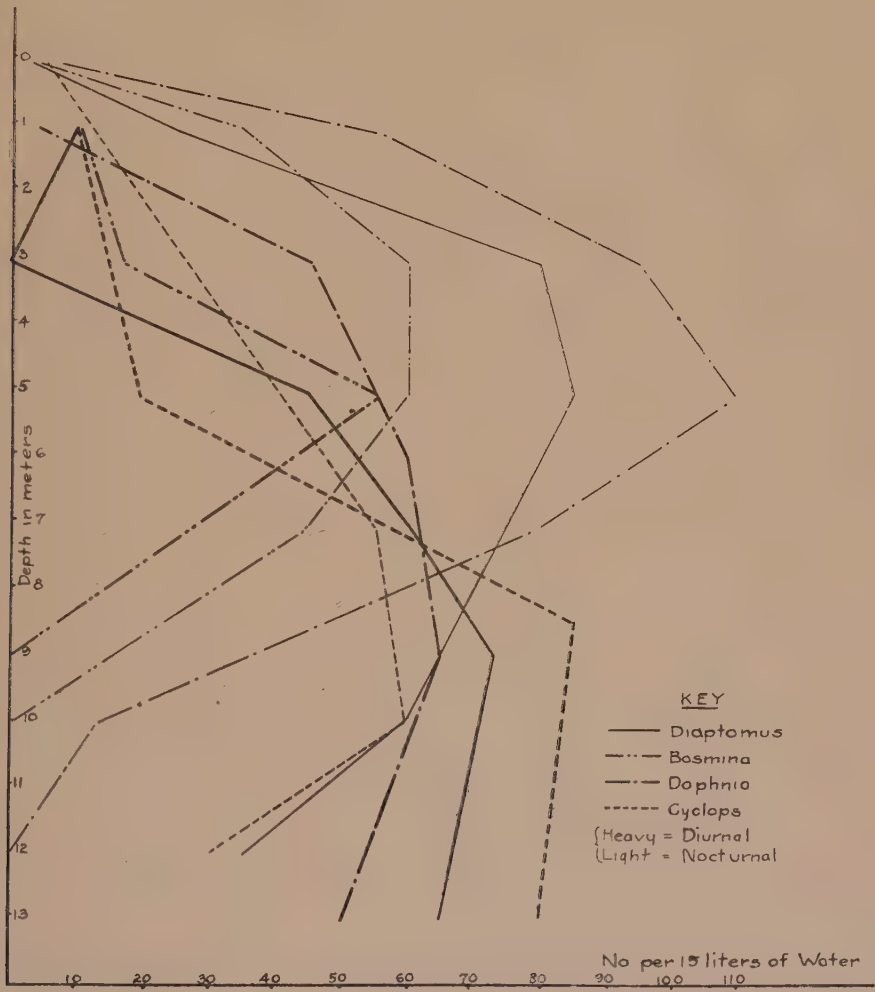




## PLATE XVI

## EXPLANATION OF PLATE XVI

FIG. 24. Showing the diurnal and nocturnal distribution in a vertical plane of certain entomostraca in Oconomowoc lake, February 2, 1916. Number of organisms represented as per 15 liters of water pumped from given depths.







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# ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XI

April, 1927

No. 2

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## FUNGI FROM COSTA RICA AND PANAMA

WITH EIGHTEEN PLATES AND A MAP IN THE TEXT

BY

FRANK LINCOLN STEVENS

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Price \$1.25

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FUNGI FROM COSTA RICA  
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WITH EIGHTEEN PLATES AND A MAP IN THE TEXT

BY  
FRANK LINCOLN STEVENS

Contribution from the  
Botanical Laboratories of the University of Illinois





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## INTRODUCTION

The fungi reported herewith were collected by the author during a period of approximately two months spent in these countries between June 20 and August 25, 1923. The actual collecting time was short, though some 70 individual trips were taken, and the collection thus represents merely a slight sampling of the richness of these very interesting regions, a sampling to be added to the earlier reports made by Pittier,<sup>1</sup> Hennings,<sup>2</sup> Patouillard,<sup>3</sup> Sydow,<sup>4</sup> Bommer and Rousseau,<sup>5</sup> and Spegazzini.<sup>6</sup>

The localities found to be especially interesting in Costa Rica are the primitive high forests near Cartago, and at La Palma, the old pass above San José; the rich jungle lying near the old railroad at Columbiana and other points, the jungle near Siquirres and the swamp jungles in the lowlands near Limon and Swamp Mouth. The high rainforest on the mountain slopes to the south of the old railroad from Siquirres to Guapiles and the jungles to the south of Siquirres hold a vast amount of very interesting material.

In Panama all may be said to be interesting. Here, as nowhere else that I know of, primitive jungle lies on all hands, only a few minutes walk from an excellent railroad, or traversed by a fine automobile road, and one may sleep and dine at comfortable hotels and spend many hours daily in primitive jungle of great richness and diversity.

The summer's collections comprise something over a thousand numbers, of which only a portion are reported herewith, the Meliolas, Microthyriaceae, rusts and many of the Ascomycetes, and many of the Fungi Imperfecti being reserved for a later paper.

As is true in most tropical collecting, the Meliolas and other Perisporiales, the Microthyriaceae, the Dothideales are especially abundant; the Phyllostictas, Septorias, Cercosporas and many other genera so common in the temperate regions, though present, are relatively rare. The smuts also are sparsely represented.

<sup>1</sup> Pittier, H., *Fungi costaricensis* I. Hedw., 41: (101), 1902.

<sup>2</sup> Hennings, P., *Einige neue Pilze aus Costarica und Paraguay*. Hedw., 43: 147, 1904.

<sup>3</sup> Patouillard, N., *Quelques champignons du Costa-Rica*. Bull. Soc. Myc. de France, 28: 140, 1912.

<sup>4</sup> Sydow, H. and P., *Novae fungorum species*, Ann. Myc., 11: 254, 1913.

<sup>5</sup> Bommer, J. E. and Rousseau, M., *Primitiae Florae Costaricensis*, Fungi. Bull. Soc. Roy. Botan. Belgique 35: 151, 1896.

<sup>6</sup> Spegazzini, Carlos, *Fungi costaricensis nonulli*. Bull. Acad. Nac. de Ciencias, Cordoba, 23: 541, 1918.

The slides, notes, original drawings and specimens on which these studies are based are deposited in the herbarium of the University of Illinois and duplicate specimens may be found in the New York Botanical Garden. The photographs reproduced in the plates were made by A. G. Eldridge; the line drawings by L. R. Tehon.

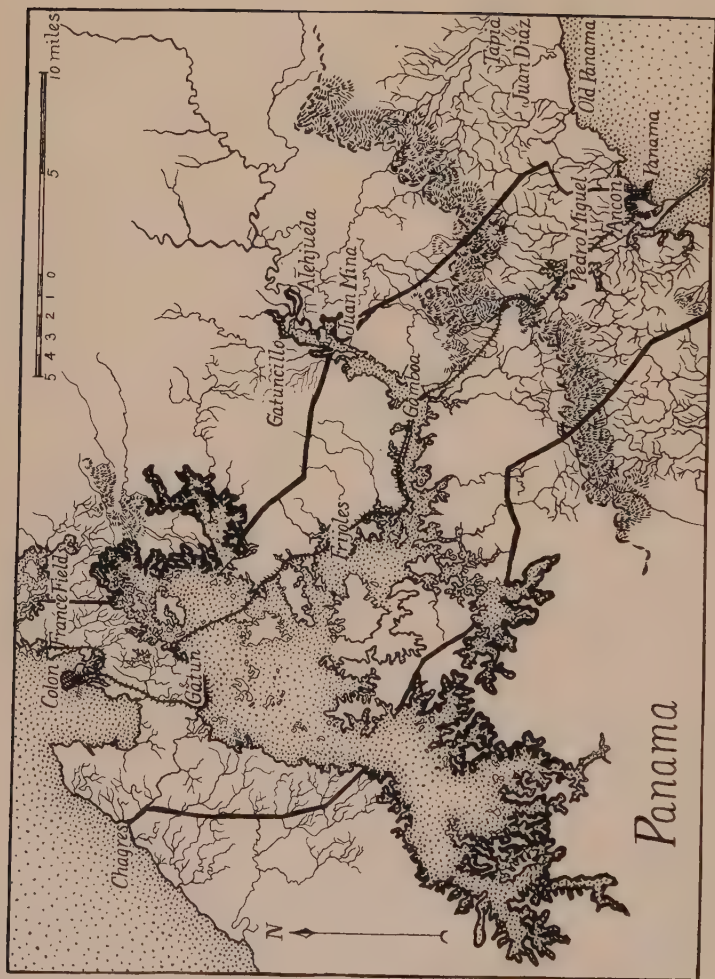
The following is a list of the field numbers with places and dates of collection.

# COSTA RICA

Nos. 1-14	San José	6-20-23
Nos. 15-26	San José	6-20-23
Nos. 27-37	Cartago	6-22-23
Nos. 38-110	Cartago	6-23-23
Nos. 111-118	San José	6-24-23
Nos. 112-118	San José	6-25-23
Nos. 119-132	Aserri	6-26-23
Nos. 133-153	Desamparados	6-27-23
Nos. 154-169	Escasu	6-29-23
No. 170	San José	6-30-23
Nos. 171-173	Guadaloupe	6-30-23
Nos. 174-179	San Vicente del Coronado	6-30-23
Nos. 180-206	Cartago	7- 2-23
No. 207	Cartago	7- 3-23
Nos. 208-217	San Pedro	7- 4-23
Nos. 218-226	Agua Caliente	7- 5-23
Nos. 227-229	Cartago	7- 6-23
Nos. 230-257	El Alto	7- 6-23
Nos. 258-270	Cartago	7- 7-23
Nos. 271-311	La Palma	7- 8-23
Nos. 312-338	Peralta	7- 8-23
Nos. 339-405	Peralta	7-12-23
Nos. 406-473	Peralta	7-13-23
Nos. 474-484	Peralta	7-14-23
Nos. 485-501	Siquirres to Guapiles	7-17-23
Nos. 502-560	Siquirres to Guapiles	7-18-23
Nos. 561-596	Siquirres to Guapiles	7-19-23
Nos. 597-616	Siquirres to Guapiles	7-20-23
Nos. 617-620	Puntarenas	7-24-23
Nos. 621-641	El Roble	7-25-23
Nos. 642-645	Conception	7-27-23
No. 646	Cartago	7-28-23
Nos. 647-648	San José	7-28-23
Nos. 649-654	Alajuela	7-29-23
No. 655		







MAP 2. SKETCH MAP OF A PART OF PANAMA SHOWING LOCALITIES  
CITED IN TEXT

No. 656	Juan Vinas	7-30-23
Nos. 657-658	Siquirres	7-31-23
Nos. 659-722	Siquirres	7-31-23
Nos. 723-735	Siquirres	8- 1-23
No. 736	Peralta	8- 1-23
No. 737	San José	8- 2-23
Nos. 738-742	Cartago	
Nos. 743-767	San Cecelia	8- 7-23
Nos. 768-772	Limon	8- 7-23
Nos. 773-783	Swamp Mouth	8- 8-23
Nos. 784-817	Sabario	8- 8-23
Nos. 818-852	Port Limon	8- 9-23
Nos. 853-892	Port Limon	8-10-23
Nos. 893-902	Port Limon	8-11-23

## PANAMA

Nos. 1000-1002	Panama	8-13-23
No. 1003	Panama	8-14-23
Nos. 1004-1057	Tapia	8-15-23
Nos. 1058-1099	Gamboa	8-16-23
Nos. 1100-1105	Pedro Miguel	8-16-23
Nos. 1106-1119	Gamboa	8-17-23
Nos. 1120-1142	Alehjuela	8-18-23
Nos. 1143-1159	Gatuncillo	8-18-23
Nos. 1160-1167	Juan Mina	8-18-23
Nos. 1168-1175	Old Panama	8-19-23
Nos. 1176-1212	Frijoles	8-20-23
No. 1213	Panama	8-20-23
Nos. 1214-1218	Panama	8-21-23
Nos. 1219-1259	Juan Diaz	8-21-23
Nos. 1260-1261	Ancon	8-22-23
No. 1262	Colon	8-23-23
Nos. 1263-1319	Chagres, 2-3 miles of Mouth	8-23-23
No. 1320	Colon	8-24-23
Nos. 1321-1340	France Field	8-24-23
Nos. 1341-1347	Gatun	8-24-23
Nos. 1348-1349	Gatun	8-25-23

It is a pleasure to acknowledge the kind coöperation received from many friends in both countries and in especial to mention the many courtesies of the United Fruit Company in Costa Rica; from Mr. G. V. Long, Mr. F. N. Cox, British Consul of San José, Sr. Francisco J. Peralta, Don Oton Jimenez of San José; and Mr. C. H. Lankester of Cartago.

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## PHYCOMYCETES

## CHYTRIDIALES

## SYNCHYTRIUM DE BARY AND WOR.

Ber. Nat. Ges. Freih. 3 H. 2:22, Schr. Krypt. Fl. Schl. Pilze 184.

## 1. SYNCHYTRIUM BOERHAAVIAE Stevens n. sp.

[Figures 1-2]

No mycelium. Resting spore globular to oval, 25 to 90 $\mu$  in diameter, double walled, inner wall hyaline, thick (7 $\mu$ ), uniform; outer wall straw colored to yellowish brown, fragile, very thin. Interior in young stages filled with vacuolate protoplasm. Sporangial sori few, thin walled, straw yellow, 90 to 110 $\mu$  in diameter. Sporangia subglobose or oval, about 25 to 28 $\mu$  in diameter, bearing numerous zoospores. Living zoospores not seen.

On *Boerhaavia erecta*.<sup>7</sup>

Costa Rica; El Roble, Sept. 25, 1923, 621.

The great variability in size of the resting spores is quite remarkable. It appears as though the small ones are fully mature since their two walls seem to be as well developed as in the larger ones. Some of the resting spores appear to contain differentiated zoospores but the evidence was not decisive.

## 2. SYNCHYTRIUM DECIPIENS Farl.

Synch. U. S., Bot. Gaz., 10:240, 1885.

On *Vigna vexillata*.

Costa Rica: Peralta, July 13, 1923, 457.

## PERONOSPORALES

## ALBUGO (Pers.) S. F. Gray

Nat. Arr. Brit. Pl., 1:540, 1821.

## 3. ALBUGO BLITI (Biv.) Kuntze.

Rev. Gen. Pl., 2:658, 1891.

On *Amaranthus* sp.

Costa Rica: San José, Aug. 2, 1923, 737.

On *Iresine acicularis*.

Costa Rica: Peralta, July 11, 1923, 314, 386, 427.

<sup>7</sup> Det. Standley.



Wilson<sup>8</sup> does not list Iresine as a host of Albugo. Conidia only were found; no oospores present.

4. ALBUGO IPOMOEAE-PANDURANAE (Schwein.) Swing.

Jour. Myc., 7:112, 1891.

On *Ipomoea* sps.

Panama: France Field, Aug. 24, 1923, 1325.

Costa Rica: San José, June 20, 1923, 2; June 21, 1923, 19; Escasu, June 29, 1923, 156; San Pedro, July 4, 1923, 209; Peralta, July 11, 1923, 332, July 13, 1923, 461; El Roble, July 25, 1923, 630; San Vicente del Coronado, June 30, 1923, 175.

5. ALBUGO PLATENSIS (Speg.) Swing.

Jour. Myc., 7:113, 1892.

On *Boerhaavia erecta*.

Panama: Frijoles, Aug. 20, 1923, 1207.

Costa Rica: Puntarenas, July 7, 1923, 619.

On *Boerhaavia caribaea*.<sup>9</sup>

Panama: Gamboa, Aug. 16, 1923, 1075.

PLASMOPARA Schroet.

Krypt. Flor. Schles. Pilze, 236, 1886.

6. PLASMOPARA Halstedii Berl. and de Toni

Sacc. Syll. Fung., 7:242, 1888.

On *Bidens* sp.

Costa Rica: Desamparados, June 27, 1923, 137; San José, June 20, 1923, 5.

On *Erechtites hieracifolia*.

Costa Rica: Peralta, July 13, 1923, 433.

ASCOMYCETES

PEZIZALES

TRYBLIDIELLA Sacc.

Sacc. Syll. Fung., 2:757, 1883.

7. TRYBLIDIELLA RUFULA (Spreng.) Syll. Fung., 2:757, 1883.

*Tryblidium rufulum* (Spreng.) Ell. and Everh. N. Am. Pyreno., 690, 1892.

*Hysterium rufulum* Spreng. in Vet. Ac. Holm., 20, 1820.

<sup>8</sup> Wilson, G. W. Studies in North American Peronosporales. Host Index. Torrey Botanical Club Bull., 35: 543, 1908.

<sup>9</sup> Det. Blake.

[Figures 92–95]

On *Citrus aurantium* (orange).

Costa Rica: Columbiana, July 20, 1923, 498.

#### HYSTERIALES

##### ACROSPERMUM Tode

Fungi Mecklenburgensis selecti, Luneburgi, 1790.

##### 8. ACROSPERMUM FOLIICOLUM Berk.

North American Fungi, no. 1000, Grevillea, 4:161, 1876.

[Figures 3, 96, 97]

On *Anthurium boltonianum*.<sup>10</sup>

Costa Rica: Sabario, Aug. 8, 807.

This fungus appears to be in every detail like the specimen of Ellis and Everhart, North Amer. Fungi, no. 2629 on decaying leaves of *Ulmus* as well as like no. 2149 on fallen leaves of Concord grape, but in all three specimens the longitudinal opening is not apparent. There is a possibility that this species should be referred to the *Hypochytrales*, possibly to *Ophionectria*, rather than to its position as given here in the *Hysteriales*.

##### LOPHODERMIIUM Chev.

Par. I. 436, De Not. Pir. Ist. 49.

##### 9. LOPHODERMIIUM ARUNDINACEUM (Schr.) Chev.

Flor. par. I. 435.

On *Andropogon bicornis*.<sup>11</sup>

Costa Rica: Peralta, July 13, 1923, 463.

#### MYRIANGIALES

##### MYRIANGINELLA Stevens and Weedon

Mycol., 15:197, 1923.

##### 10. MYRIANGINELLA COSTARICENSIS Stevens n. sp.

[Figures 4, 5]

Spot pale, subcircular, indefinite, surrounding the stromata, showing from both leaf surfaces. Stromata solitary, hypophyllous, raised above the leaf surface, brown to black, fastened by a central brown foot about  $140\mu$  wide which extends a short distance into the mesophyll and also occupies the epidermal cells. Stroma brown, without definite boundary,  $460$  to

<sup>10</sup> Det. Standley.

<sup>11</sup> Det. Chase.

620 $\mu$  in diameter, up to 310 $\mu$  deep. Asci solitary, 8-spored, inordinate, 83 to 93 x 25 $\mu$ . Paraphyses matted densely, above forming a brown epithecium. Spores hyaline, muriform, 5 to 6 cross or oblique walls, 25 to 32 x 7 to 9 $\mu$ , obtuse.

On *Miconia* sp.

Costa Rica: Siquirres, July 31, 1923, 698.

Thus fungus is quite similar to *Myrianginella tapirae* in its superficial parts but differs essentially in the foot and hypostroma as well as in spore size and septation; it differs from *Myriangina* in the generic characters, also in spore shape and septation.

#### PERISPORIALES

#### PERISPORIACEAE

#### Key to genera included herein

- Subcuticular stroma present.....Pseudoparodiella p. 14
- Subcuticular stroma not present—Perithecia and mycelium superficial, nonhyphopodiate
  - Spores filiform.....Tonduzia p. 16
  - Spores not filiform
    - Setae present
      - Spores hyaline, 2-celled
        - Asci aparaphysate.....Dimeriella p. 16
        - Asci paraphysate.....Chaetostigme p. 17
      - Spores hyaline, 3-celled.....Dimeriellopsis p. 17
      - Spores brown, 4-celled.....Hyalomeliolina p. 18
    - Setae absent or atypical, perithecium smooth
      - Spores colorless, 2-celled
        - Perithecium dark.....Dimerina p. 19
      - Spores brown, 2-celled
        - Perithecia red.....Parodiopsis p. 19
        - Perithecia dark.....Parodiella p. 19
      - Spores brown, 3-celled.....Perisporina p. 19
      - Spores brown, 4-celled.....Perisporium p. 20

#### PSEUDOPARODIELLA Stevens n. gen.

Fungus Perisporiaceous, asci paraphysate, no external mycelium, stroma subcuticular, conidiiferous. Perithecia free, globose, borne on a subcuticular stroma, setose. Asci 8-spored, spores 2-celled, hyaline.

#### 11. PSEUDOPARODIELLA VERNONIAE Stevens n. sp.

[Figures 6–15, 98]

Spots circular or irregular, indefinite, 0.5 to 1 cm. in diameter, visible from both leaf surfaces as dead or bleached tissue. Surface covered, above

or below, or both, with black conidia. No external mycelium. Stroma subcuticular, thin, about 3 to 9 $\mu$ , usually one, sometimes 2 to 3 cells in thickness, erumpent through the cuticle. Perithecia globose, about 90 $\mu$  in diameter, attached to the stroma by a base about 30 $\mu$  broad, 15 $\mu$  high, bearing setae, about 13 on each perithecium. Setae obscurely septate, brown at base, pale toward tip, obtuse, 21 to 126 x 7 to 8 $\mu$ . Asci 8-spored, oblong, short stalked, 52 to 70 x 17 $\mu$ , spores inordinate. Paraphyses filiform. Spores 17 x 3 $\mu$ , hyaline, 1-septate, not constricted, thicker at the middle, tapering toward each end. Conidiophores short, 3 x 7 $\mu$ , (or longer, 18 $\mu$ ) arranged in a compact, low tubercle, dark on distal end, less dark on proximal end. Conidia ovoid or elliptical, dark, catenulate, in rows up to five or more, usually continuous and about 11 x 7.5 $\mu$ , occasionally larger, 11 x 18 $\mu$ , and 1-septate.

On *Vernonia canescens*.<sup>12</sup>

Costa Rica: Peralta, July 12, 1923, 352.

The general aspect of this fungus to the naked eye is that of *Parodiella* or related genera (Fig. 98) but celloidin or scrape mounts give only large quantities of the catenulate conidia (Fig. 12) which give the appearance of a dematoid mycelium (Fig. 14). Microtome sections reveal a subcuticular, hyaline, or nearly hyaline, mycelium one cell in thickness. (Fig. 13.) Views from the surface show this subcuticular mycelium to be arranged in bands composed of several, usually 1 to 6, parallel mycelial threads (Figs. 6, 8, 11) which do not appear to extend for any considerable distance. At very frequent intervals on this subcuticular thallus the cells elongate vertically producing a very low tubercle, usually only 5 to 8 cells in diameter and about 7 $\mu$  high, which is conidia-bearing (Fig. 13). Often also the tubercle becomes somewhat higher, 18 $\mu$ , by elongation of its component conidiophores (Fig. 13). The conidia in short chains are shown in Fig. 14. The 1-septate conidia are comparatively rare and may occur anywhere in a chain, either terminal or intercalary. The perithecia are borne on low tubercles quite like those that bear the conidia.

The perithecium, without ostiole, appears Perisporiaceous. The subcuticular stroma in section is of distinctly Dothideaceous aspect, but relationship with the Dothids is not borne out by any other characters, and indeed is denied by the free superficial perithecia. The subcuticular, thin stroma, composed of bands of parallel mycelium (Figs. 6, 8, 11) reminds one strongly of the subcuticular mycelium of *Actinonema rosea*, also to some extent of *Fusicladium*. In the Perisporiaceae as given by Lindau<sup>13</sup> this fungus would fall close to *Parodiella*. In the key of Theissen and Sydow<sup>14</sup> it would fall close to *Alina* but is quite distinct from it in

<sup>12</sup> Det. Standley.

<sup>13</sup> Engler and Prantl, *Die Naturlichen Pflanzenfamilien*, T. 1., Ab. 1:333, 1897.

<sup>14</sup> *Ann. Myc.*, 15:459, 1917.



being without hairs, in the color of the spores, in the nature of the sub-epidermal subiculum and its conidia. *Parodiella* is excluded from the Perisporiaceae by Theissen and Sydow<sup>15</sup> as belonging to the Pseudosphaeriaceae which are characterized by locules with solitary asci, or by asci separated by a pseudoparenchyma. Our fungus does not possess this character but does have the asci separated by paraphyses. Arnaud<sup>16</sup> sets up the tribe Parodiellineae, in the family Parodiellinaceae, characterized by a unilocular stroma and by the absence of external mycelium. In this family our species is most nearly related to *Parodiellina* P. Henn. The differences from this are however very marked, particularly in the thin subcuticular stroma.

The subcuticular stroma, reminding one strongly of the *Trabutineae*, but bearing conidia profusely; the resemblance to *Actinonema* when viewed from above; the general aspect of *Parodiella* and its kin; the Perisporiaceae perithecium all present a series of anomalous characters which render it difficult to assign to this fungus a definite position in present systems of classification.

*TONDUZIA* Stevens n. gen.

Perisporiaceae, superficial, non-hyphopodiate, perithecium and mycelium non-setose. Spores filiform; no paraphyses. Named in honor of Sr. Adolfo Tonduz.

12. *TONDUZIA PSYCHOTRIAE* Stevens n. sp.

[Figures 16, 17a, 17b]

Fungus superficial, hypophyllous, black, colonies subcircular, about 1 cm. in diameter. Mycelium brown, non-hyphopodiate, smooth. Perithecia up to 140 $\mu$  in diameter, subglobose, black, rough. Asci linear, cylindrical, obtuse, 47 to 72 x 7 $\mu$ , short stipitate, paraphysate. Spores filiform, hyaline, 46 to 65 x 1.7 $\mu$ , obtuse, several septate, guttulate.

On *Psychotria brachiata*.<sup>17</sup>

Costa Rica: Columbiana, July 19, 1923, 570.

This fungus is clearly Perisporiaceae and is remarkable chiefly for its filiform spores, which are exceedingly rare in this family.

*DIMERIELLA* Speg.

Fungi aliquot Paulistani, in *Revista del Museo de La Plata*, 15:1908.

13. *DIMERIELLA OLYRAE* Stev.

Trans. Ill. Acad. Sci., 10:167, 1917.

On *Olyra latifolia*.

<sup>15</sup> Theissen F. and Sydow. H. Vorentwurfe zu den Pseudosphaeriales. *Ann. Myc.*, 16:6, 1918.

<sup>16</sup> Arnaud G. Les Asterineae, *Ann. d. Epiphyties.*, 7:45. 1921.



Panama: Alehjuela, August 18, 1923, 1121.

Costa Rica: Peralta, July 11, 1923, 315.

CHAETOSTIGME Syd.

Ann. Myc., 15:199, 1917.

14. CHAETOSTIGME CORDIAE (P. Henn.) n. comb.

[Figure 18]

The genus *Chaetostigme* described as above cited appears to be valid and desirable to receive the paraphysate forms previously placed in the genus *Dimeriella* Speg., though Theissen and Sydow do not recognize this genus in their *Synoptische Tafeln*.

*Dimerosporium cordiae* P. Henn. Fungi S. Paulenses IV. in Hedw., 48:4, 1908.

*Dimeriella cordiae* (P. Henn.) Theiss. Zur Revision der Gattung *Dimerosporium* in Bot. Cent. Beihefte, 29:67, 1912.

On *Cordia interrupta*.<sup>18</sup>

Costa Rica: Port Limon, August 11, 1923, 901, 902.

On *Cordia corymbosa*.<sup>18</sup>

Costa Rica: Peralta, July 11, 1923, 316, 324.

On *Cordia* sp.

Costa Rica: Guapiles, July 20, 1923, 561.

This species was selected by Theissen and Sydow to be the type of the genus *Dimeriella* Speg., a procedure which if followed would make *Dimeriella* paraphysate, since *D. cordiae* is paraphysate. However, since Spegazzini describes *Dimeriella hirtula*, and that species alone, in connection with his generic description,<sup>19</sup> *D. hirtula* and not *D. cordiae* is the type of the genus *Dimeriella*; and since *D. hirtula* is aparaphysate the genus *Dimeriella* is aparaphysate. *Dimerosporium cordiae* P. Henn. therefore becomes *C. cordiae* as indicated above.

15. CHAETOSTIGME ERIGERONICOLA (Stev.) n. comb.<sup>20</sup>

*Dimeriella erigeronicola* Stev. Trans. Ill. Acad. Sc., 10:166, 1917.

On *Erigeron* sp.

Costa Rica: Peralta, July 13, 1923, 448; Los Mercedes, July 17, 1923, 488.

DIMERIELLOPSIS Stevens n. gen.

Fungus superficial; mycelium not dematioid, not gelatinous, non-hyphopodiate. Perithecia setose, spores 3-celled, hyaline.

<sup>17</sup> Det. Standley.

<sup>18</sup> Det. Standley.

<sup>19</sup> Fung. aliquot Paulistani p. 12 in Revista del Museo de La Plata, 15, 1908.

<sup>20</sup> This, according to Sydow (Ann. Mycol., 24:335, 1926), is of the *Pseudosphaeriaceae* and he regards it as belonging to the genus *Lasiostemma*.

## 16. DIMERIELLOPSIS COSTARICENSIS Stevens n. sp.

[Figures 19, 99]

Mycelium superficial, straw colored, very thin ( $1\mu$ ), not dematioid nor gelatinous. Perithecia superficial, dark brown, globose, 90 to  $150\mu$  in diameter, without ostiole, or ostiole atypical, bearing numerous setae ( $70\mu$ ), long (up to  $460\mu$ ),  $5\mu$  thick at base, translucent, straw-colored. Asci 8-spored, inordinate. Spores hyaline, fusiform, 2-septate, 21 to 32 x 6 to  $7\mu$ .

On *Canavalia* sp.<sup>21</sup>

Costa Rica: Swamp Mouth, August 8, 1923, 783.

This fungus is clearly Perisporiaceous and is distinguished from *Dimeriella* in the key of Theissen and Sydow by spore septation. It also differs very strikingly from that genus in the character of its perithecial setae. (Fig. 99.)

Numerous septate conidiophores, 100 to  $200\mu$  x  $3.5\mu$ , bearing oblong, straw-colored, septate conidia ( $55 \times 3.5\mu$  or shorter) occur on many of the colonies. These conidiophores may represent a parasite on the other fungus or they may be genetically connected with it. The perithecial setae arise as outgrowths of single perithecial wall cells.

## HYALOMELIOLINA Stevens

Ill. Biol. Monog., 8:27, 1923.

## 17. HYALOMELIOLINA COSTARICENSIS Stevens n. sp.

Colonies superficial, black, circular, 3 to 10 mm. in diameter, hypophyllous. Mycelium black, smooth, non-hyphopodiate, uniform in diameter,  $4\mu$ , slightly crooked, very sparsely branched. Perithecia numerous, not enveloped in mycelium, globose, black,  $150\text{--}262\mu$  in diameter, slightly rough, bearing many black, simple, septate setae, about  $4\mu$  in diameter, 300 to  $800\mu$  in length, mycelium-like. Asci persistent,  $150 \times 40\mu$ , usually 8-spored, stipitate, ovate, thick-walled. Spores inordinate, elliptical-fusoid, dark, 47 to 54 x 17 to  $18\mu$ , unequally 3-septate, constricted at the central septum. Two end cells very small and hyaline; central cells brown.

On *Tetracera volubilis*<sup>22</sup>

Costa Rica: Squirres, July 31, 1923, 668 (type).

This fungus is clearly cogeneric with *Hyalomeliolina guianensis* Stevens<sup>23</sup> but differs from it in that the perithecia are not buried in mycelium but are in very sparse mycelium. The mycelium is not ropy as in the other species. The asci and spores are also somewhat larger. These two species

<sup>21</sup> Det. Standley.

<sup>22</sup> Det. Standley.

<sup>23</sup> Stevens, F. L., Parasitic Fungi from British Guiana and Trinidad. Ill. Biol. Monog. 8:No. 3, 1923.

are sufficiently different from *Meliolina* to warrant making for them a separate genus.

DIMERINA Theissen

Beihefte Bot. Cent., Ab. 2., 29:46, 1912.

18. DIMERINA DODONAEAE Stevens n. sp.

[Figures 20, 100]

Fungus superficial, hypophyllous. Perithecia globose, about  $45\mu$  in diameter, smooth, yellow to black, very numerous in groups. Asci 8-spored, globose to ovate or clavate,  $22$  to  $30 \times 11$  to  $14\mu$ . Paraphyses none. Spores hyaline, oblong,  $14$  to  $3\mu$ , 1-septate, rarely 2-septate.

On *Dodonaea viscosa*<sup>24</sup>

Costa Rica: Swamp Mouth, August 8, 1923, 780.

Of the sixteen species given by Theissen only three agree reasonably in spore and perithecium size with ours, viz. *D. galactis* (E. & E.) Th., *D. negeriana* (P. Henn.) Th., and *D. minutissimum* (V. Höhn) Th. The first of these disagrees in the possession of yellow spores; the second in spore shape and widely distinct host; the third in location on leaf, shape of perithecium and spores.

PARODIOPSIS Maub.

Bull. Soc. Myc., France, 31:3, 1915.

19. PARODIOPSIS INGARUM (P. Henn.) Arn.

On *Inga* sp.

Panama: Chagres River 2–3 mi. from mouth, August 23, 1923, 1275.

PARODIELLA Speg.

Fungi Arg. Pug., I. 178.

20. PARODIELLA PERISPORIOIDES (Berk. and Curt.) Speg.

Fungi Arg. Pug., 1, 178, 1880.<sup>25</sup>

On *Stylosanthes* sp.

Costa Rica: Peralta, July 12, 1923, 345.

PERISPORINA P. Henn.

Hedw., 43: 357, 1904.

21. PERISPORINA DENTRITICA Stevens n. sp.

[Figures 21–23]

Spot subcircular, pale, indefinite, 2 to 5 cm. in diameter, visible from both leaf surfaces, mycelium hypophyllous, straw colored, cells long,

<sup>24</sup> Det. Standley.

<sup>25</sup> This is regarded by Sydow as *Hypoplegma viridescens* (Rehm) Th. & Syd.

cylindrical, minutely echinulate. Perithecia globose, superficial, black, slightly rough by conical prominences about  $7\mu$  high, 155 to  $215\mu$  in diameter, non-ostiolate. Asci  $145 \times 44\mu$ , ovate, thick walled, thickened at apex. Paraphyses none. Spores  $61 \times 14\mu$ , oblong, tapering from the middle, 3-septate, hyaline, rounded at apex, truncate at base. Mycelial setae dendritically, intricately branched.

On *Inga* sp.

Costa Rica: Experiencia Farm, July 18, 1923, 517.

This fungus in its superficial mycelium and perithecia has the habit of a Parodiopsis, but is striking for the large diseased spot that it produces, also for its tan colored mycelium merging to hyaline in the outer, younger parts of the colony. The setae arise directly from the echinulate mycelial cells. They may be absent from large portions of a colony or present in great abundance, especially in the older portions. I venture to place this fungus in this genus, though the only spores seen were hyaline, due to its obvious, close relationship to *P. manaosensis*.

Several other species of fungi were present in abundance in the colonies, evidently parasitic upon the Perisporina.

#### PERISPORIUM Fr.

Syst. Myc., 3:248.

#### 22. PERISPORIUM BROMELIAE Stev.

Ill. Trans. State Acad. Science, 10:162.

On *Bromelia pinguin*.

Costa Rica: Asarri, June 26, 1923, 132.

#### CAPNODIACEAE

#### CERATOCHAETOPSIS Stevens and Weedon n. gen.

Capnodiaceous, perithecium globose, sessile, mycelium and perithecium superficial, gelatinous, mycelium without setae, perithecium setose, spores 2-celled, hyaline.

#### 23. CERATOCHAETOPSIS COSTARICENSIS Stevens and Weedon n. sp.

Mycelium epiphyllous, superficial, yellow, translucent, not beaded, very thin, gelatinous, forming a loose network. Perithecia globose, solitary,  $98$  to  $138\mu$  in diameter, yellow to brown, darker than the mycelium. Perithecial setae  $42$  to  $91 \times 7$  to  $10\mu$ , curved, pale yellowish green when young, brown when old, slightly pointed to rounded at tip, usually 8 to 12 in number. Asci  $21$  to  $38 \times 7$  to  $10\mu$ , 8-spored. Spores  $14$  to  $21 \times 2.4$  to  $3\mu$ , 1-septate, hyaline, many guttulate, fusiform, sometimes slightly curved, ends rounded.

On *Myrcia costaricensis*.<sup>25</sup>

Costa Rica: La Palma, July 8, 1923, 908.

<sup>25</sup> Det. Standley.



This fungus is clearly Perisporiaceous and falls, according to the key of Theissen and Sydow, next to the genus *Ceratochaete* from which it differs in the possession of no mycelial setae. It is found as barely visible reddish or yellowish groups of perithecia on the surface of the host leaves.

## HYPOCREALES

## BALANSIA Speg.

Fung. Guar. Pug., 1 n. 253, 1883.

24. BALANSIA DISCOIDEA P. Henn.<sup>27</sup>

Hedw., 39:(77), 1900.

On *Panicum haenkeanum*.<sup>28</sup>

Costa Rica: Siquirres, July 31, 1923, 694.

## DOTHICHLOE Atkinson

Bull. Torr. Bot. Club, 21:223, 1894.

25. DOTHICHLOE ATRAMENTOSA (B. & C.) Atk.<sup>29</sup>

Jour. Myc., 11:259, 1905.

*Hypocrea atramentosa* B. & C., Jour. Linn. Soc., 10:377, 1869.

*Hypocrella atramentosa* Sacc., Mich., 1, 323, 1878.

On *Sporobolus berterioanus*.<sup>30</sup>

Costa Rica: San José, June 20, 10, June 21, 17, June 24, 111;  
Desamparados, June 27, 151; Escasa, June 29, 157.

## SPHAEROSTILBE Tul.

Carpol., 3:103.

26. SPHAEROSTILBE COCCOPHILA Tul.<sup>31</sup>

Carpol., 3:105.

On *Citrus aurantium*, Orange.

Costa Rica: Columbiana, 500.

## DOTHIDEALES

## Key to genera included herein

Stroma radial . . . . .	Polystomellaceae p. 23
Locules linear . . . . .	Cocconia p. 23
Locules circular, no free mycelium . . . . .	Polystomella p. 23
Locules in a superficial, strap-shaped stroma. .	Rheumatopeltis p. 24

<sup>27</sup> Det. W. W. Diehl.

<sup>28</sup> Det. Mrs. Agnes Chase.

<sup>29</sup> Determined by W. W. Diehl.

<sup>30</sup> Host determined by Mrs. Agnes Chase.

<sup>31</sup> Det. Seaver.



## Stroma not radial

- Stroma dothideoid, superficial or erumpent... Dothideaceae p. 25
- Stroma superficial, centrally fastened..... Coccoideae p. 25
- Stroma fertile throughout.....
  - Spores 1-celled.....
    - Spores needle-formed..... Schweinitziella p. 25
    - Spores filiform..... Scolecoccoidea p. 26
    - Spores elliptical, hyaline, paraphysate..... Coccostromopsis p. 27
- Stroma erumpent..... Dothideae p. 27
  - Spores 1-celled, hyaline, perithecia not beaked..... Bagnisiopsis p. 27
  - Spores 1-celled, hyaline, perithecium beaked..... Hyperus p. 27
  - Spores 1-celled, brown..... Dothidina p. 28
  - Spores 2-celled, brown, paraphysate... Achorella p. 29
- Stroma remaining covered..... Phyllachoraceae p. 3
- Stroma between cuticle and epidermis..... Trabutinee
  - Spores 1-celled, hyaline
    - Paraphysate..... Trabutia p. 30
    - Aparaphysate..... Hypostigma p. 31
  - Spores equally 2-celled, hyaline, aparaphysate..... Euryachora p. 31
- Stroma between epidermis and palisade... Schirrhiineae p. 31
- Stroma not linear, spores 1-celled, hyaline.
  - unappendaged, paraphysate..... Catacouma p. 31
- Stroma linear, spores unequally 2-celled, hyaline, paraphysate..... Apiospora p. 32
- Stroma in the mesophyll..... Phyllachorineae p. 33
  - Spores 1-celled
    - Spores hyaline
      - Paraphysate..... Phyllachora p. 33
      - Aparaphysate..... Phyllachorella p. 41
    - Spores brown, paraphysate..... Sphaerodothis p. 42
  - Spores equally 2-celled, brown, paraphysate..... Phaeodothis p. 43
  - Spores 4-celled, hyaline, aparaphysate..... Phragmocarpella p. 44
  - Spores filiform..... Ophiodothella p. 44
- Loculi isolated, perithecium-like..... Montagnellaceae p. 45
  - Spores 1-celled, hyaline, paraphysate.. Haplothecium pp. 45
- Conidia only..... Pycnidiostroma p. 45

## POLYSTOMELLACEAE

## COCCONIA Sacc.

Syll. Fung., 8:738, 1889.

## 27. COCCONIA PALMAE Stevens n. sp.

[Figure 24]

Fungus chiefly epiphyllous, black, 1 to 3 mm. across, opposite side of leaf usually showing a discolored spot, sometimes with stromata on both leaf surfaces. Superficial stromata radiate, bearing several linear perithecia that are very irregularly, concentrically arranged. Hypostroma extending deep into the mesophyll, attached to the superficial parts at several points. Locules globose or somewhat flattened, 150 to 170 x 60 to 80 $\mu$ . Asci 8-spored. Paraphyses filiform. Spores dark, equally 2-celled, oblong, constricted, 14 x 3 $\mu$ .

On palm.

Costa Rica: Peralta, July 13, 1923, 432.

The loculiferous stroma occurs either as the superficial stroma or on the erumpent stroma. The circular arrangement of the perithecia is so irregular that the suggestion of this as a character is questionable.

This fungus is of special interest as a form showing the characters of the Microthyriaceae in the radiations of the superficial stroma, and of the Dothideales in possessing globose locules in a stroma.

## POLYSTOMELLA Speg.

F. Guaran. 2:51, No. 137, 1888.

## 28. POLYSTOMELLA COSTARICENSIS Stevens n. sp.

[Figures 25, 26, 101, 102]

Stromata superficial, amphigenous, 230 to 245 $\mu$  thick, 1000 to 1600 $\mu$  broad, circular, edge rising abruptly from the leaf surface. Surface when young marked by concentric furrows, when older also by radial fissures; color dull black. Stroma bordered on sides and top by a black rind about 15 $\mu$  thick, composed of pseudoparenchyma. Context of pale thin-walled pseudoparenchyma which further toward the center becomes hyaline and gelatinous, filamentous. Hypostroma consisting of thick, dark mycelium filling certain of the epidermal cells. Locules numerous, ovate, about 90 to 110 $\mu$  wide, 150 to 170 $\mu$  deep, without definite boundary. Interlocular tissue composed of gelatinous filaments much resembling the paraphyses. Asci numerous, 8-spored, cylindrical, with a long, crooked stipe, 100 x 18 $\mu$  or larger. Spores oblong, hyaline, 2-celled, slightly constricted, obtuse, 18 to 19 x 5 to 7 $\mu$ . Paraphyses filiform, gelatinous. Conidial cavities oval to cylindrical or irregular, sometimes reaching from the base to the top of a stroma occur. Conidia very minute, about 1 $\mu$  in diameter, oval, hyaline, continuous, borne on the tips of filiform conidiophores.

On *Siruthanthus* sp.

Costa Rica: El Alto, July 6, 1923, 255 (type); Cartago, June 23, 1923, 97.

The covering layer is radiate, though on account of the dense color and hardness it is only with difficulty that this character is observable. Fragmentation of the covering layer occurs at the apices of the locules affording means of spore escape without the development of actual ostioles. The stroma is not anchored to the epidermal cells throughout its base but often only near the edge, leaving the central part without attachment.

This fungus agrees well with *Polystomella* as described. Prominent characters are the surface markings of the stromata, concentric and radial cracking and the peculiar gelatinous hyphal structure between the locules. The surface view shows distinct radiation, so characteristic of the Microthriaceae while the stroma in vertical section, near its edge, is distinctly dothideoid, as are also the locules, in that they are without definite walls. The interlocular context differs markedly from the Dothideales. Showing affinities with both the Dothideales and the Microthyriaceae, yet differences from each of them the fungus is of special interest.

The present species differs from *P. crassa* in the shape of the stroma, location of the conidial locules; from *P. pulcherrima* because the asci are larger, also because there is great difference in the mode of occupation of the epidermis (c.f. Fig. 26 with T. VI Fig. II Ann. Myc., 12); from *P. salvadorae* in shape of locules; from *P. granulosa* in character of hypostroma; from *P. pulchella* in shape of stromata and size of spore; conidial loculi are mentioned in connection with *P. crassa* (Rehm) Theiss. but no description of the conidia is given. The cells described as conidia here are very small and perhaps functionless.

#### RHEUMATOPELTIS Stevens n. gen.

Plant body composed of a superficial, strap-shaped mycelial thallus bearing locules in dothideoid stromata. Asci 8-spored, paraphysate, spores falcate, continuous, fuscous. Name from *ῥεῦμα* stream.

#### 29. RHEUMATOPELTIS QUERCI Stevens n. sp.

[Figures 27-31, 103, 104]

Superficial thallus epiphyllous, strap-shaped, composed of parallel threads, radiating at the ends and somewhat at the sides of the bands. Stromata dothideoid. Locules 185 to 215 $\mu$  broad, 80 $\mu$  deep, usually solitary in each loculiferous region of the stroma, ostiolate. Asci 8-spored, ovate, thin walled, 47 x 14 to 18 $\mu$ , basally borne. Paraphyses filiform, gelatinous, crooked, long, slender, many. Spores 1-celled, fuscous when mature, straight, or falcate, acute at each end, 18 to 29 x 3 to 4 $\mu$ .

On *Quercus eugenifolia*.<sup>32</sup>

Costa Rica: Cartago, June 23, 1923, 68.

The thallus is composed of anastomosing, strap-shaped bands, each about  $150\mu$  broad, the whole colony occupying an area a centimeter or more in diameter. In section the straps are seen to be superficial and several (3 to 4) cells in thickness. At frequent intervals the thallus develops into thickened regions which are genuine stromata of typical dothideoid structure (Fig. 28). The epidermal cells below the thallus are usually filled with mycelium. The floor of the locule is thin, dark, and in structure generally like the extra-loculiferous bands.

This fungus, in the structure of the stroma, is strictly Dothideaceae and possessing a radiating superficial mycelium would appear to fall within the Polystomellaceae. The strap-shaped bands of the thallus remind one strikingly of the Trichopeltaceae but the cell structure is quite different from that found in that family, in that cell plates, one cell in thickness, are not formed but the thallus is clearly mycelial in character though assuming the form of bands. The fungus as regards the characters given in the keys appears to fall nearest to *Ellisiodothis* from which it is separated by its fuscous spores. Its thallus body is however very distinct from that fungus.

#### DOTHIDEACEAE

#### COCCOIDEAE

#### SCHWEINITZIELLA Speg.

F. Guaran., 2: no. 119, 1888.

#### 30. SCHWEINITZIELLA PALMIGENA Stevens n. sp.

[Figures 32, 33]

Spot small, consisting only of a very narrow, yellowish, translucent zone surrounding the stromata, subglobose, visible from below also as darkened areas. Stromata black, superficial, rough, small, (1 mm. in diameter, about 0.2 to 0.6 mm. high), epiphyllous, centrally fastened to the leaf by a foot that is of pseudo-palisade structure. Hypostroma completely occupying the epidermal cells with a dark mycelium, eventually similarly occupying all cells below the stroma. Stroma bordered by a dark rind, 18 to  $36\mu$  thick. Interior of stroma hyaline, cells thin-walled, gelatinous. Locules in young stromata regularly disposed midway between the cortex and foot, in old stromata irregularly arranged, globose, subglobose, flattened or irregular, 77 to  $185\mu$  in diameter, bounded by a thin wall of very slightly darkened cells. Ostioles well developed. Asci clavate, 43 to  $61 \times 7$  to  $11\mu$ , short stipitate, 8-spored. Spores hyaline, slender, crescent-

<sup>32</sup> Det. Wm. Trelease.



shaped, acute at each end, continuous, 36 to 47 x 3 $\mu$ . Paraphyses filiform, very thin, gelatinous.

On *Chamaedorea* sp.<sup>33</sup>

Costa Rica: Peralta, July 13, 1923, 417, accompanied also by *Coccostromopsis palmigena*.

The stroma structure here is exceptionally interesting. The foot of the stroma shows a faint, barely perceptible, palisade arrangement. As the central region of the stroma is approached the palisade arrangement is lost and the cells become more and more pale and more gelatinous.

This fungus is clearly related to the Dothideales as is evidenced by its general aspect, the character of the hypostroma and the central fastening of the stromata to the leaf and particularly the evident, though not too-well marked prosenchymatic, palisade cell arrangement in the stipe of the stroma. It differs from the typical Dothid in that there is a faint wall within the stroma and surrounding the locules. This wall is however no more pronounced than is that found in many Dothids. A second point of deviation from the Dothids is in the cell structure of the stroma, a large portion of the more central region of the stroma being composed of hyaline, gelatinous, tangled filaments such as I have seen in no other Dothid and which have lost all semblance of palisade arrangement. This makes this species stand out as quite exceptional. It clearly belongs to the Coccoideae of the Dothideaceae, close to *Schweinitziella* and *Coccostroma*. From the latter of these it is excluded by the possession of paraphyses. The stroma type is clearly very different from that of *Schweinitziella* and probably warrants placing it in a new genus but I am at present reporting it under the above name.

The central fastening of the epistroma by a cylindrical foot reminds one strongly of the structure found in *Bagnisiopsis* and in the Coccoideae, but the foot differs from those usually seen in that it is pale, brown to hyaline, in portions and that it is not of characteristic dothideoid structure. While it gives suggestions of palisade arrangement in places it also is very irregularly organized elsewhere. It clearly belongs in the Dothideaceae either in the Coccoideae or the Dothideae of which it shows closer kinship with the former. In neither of these groups are genera with filiform spores.

#### SCOLECOCOIDEA Stevens n. gen.

Fungus of the Coccoideae, stroma loculiferous throughout, spores filiform.

#### 31. SCOLECOCOIDEA COSTARICENSIS Stevens n. sp.

[Figure 34]

Spot none or merely consisting of a slight yellowing of the leaves around the stromata. Stroma hypophyllous, punctiform (0.5 mm.), black, showing

<sup>33</sup> Det. O. F. Cook.



on the surface contours of numerous (30 to 40) perithecia, centrally fastened. Hypostoma consisting of a foot about  $180\mu$  in diameter extending about half way through the leaf ( $125\mu$ ), pale or brown, slightly dothideoid in character. Epistroma about 600 to  $800\mu$  in diameter, locules at one level, separated by a thin, pale to yellow, boundary. Locules subglobose, about  $150\mu$  in diameter. Asci 8-spored, long, slender,  $108$  to  $144 \times 2\mu$ . Paraphyses filiform. Spores filiform, extremely thin,  $80 \times 0.7\mu$ .

On *Miconia* sp.

Costa Rica: Parismina Junction, July 20, 1923, 603.

#### COCCOSTROMOPSIS Plunkett

Ill. Biol. Monog. 8:10, 1923.

#### 32. COCCOSTROMOPSIS PALMIGENA Plunkett

Ill. Biol. Monog., 8:10, 1923.

On *Chamaedorea* sp.<sup>34</sup>

Costa Rica: Peralta, July 13, 1923, 417, accompanied by *Schweinitziella palmigena*.

#### DOTHIDEAE

#### BAGNISIOPSIS Theiss. and Syd.

Ann. Myc., 13:291, 1915.

#### 33. BAGNISIOPSIS PERIBEBUYENSIS (Speg.) Theiss. and Syd.

On one of the Melastomataceae.

Costa Rica: Peralta, July 12, 1923, 379; La Palma, July 8, 1923, 277.

On *Miconia* sp.

Panama: Gamboa, Aug. 16, 1923, 1072 and 1096; Gatun, Aug. 24, 1923; France Field, Aug. 24, 1923, 1326; Chagres mouth Aug. 23, 1923, 1317.

Costa Rica: La Palma, July 19, 1923, 294.

#### HYPERUS Stevens n. gen.

Stromata hypophyllous, erumpent; hypostroma permeating the mesophyll. Perithecia dark walled, immersed in the stroma, ostiolate and beaked. Asci 8-spored; spores cylindrical, hyaline, continuous. Genus name from ὑπεροδ, pestle.

#### 34. HYPERUS COSTARICENSIS Stevens n. sp.

[Figures 35-40, 105]

Hypostroma extensive in the mesophyll. Stromata erumpent, brown to yellow, rising 150 to  $230\mu$  above the leaf surface, 80 to  $230\mu$  thick, usually thicker above than at the base. Locules globose or elongate, up

<sup>34</sup> Det. O. F. Cook.

to  $290\mu$  in diameter, bounded by a definite, dark wall about  $30\mu$  thick. Ostiole in a beak  $150$  to  $200 \times 46$  to  $60\mu$ . Asci numerous, very small,  $22 \times 5.5\mu$ . Spores short, cylindrical, hyaline, continuous,  $5.5 \times 1.5\mu$ .

Conidial locules borne in stromata similar to those of the ascigerous locules but smaller. Locules subglobose up to  $180\mu$  in diameter, locular wall less dark and definite than that of the ascigerous locules. Conidio-phores straight, simple, about  $25 \times 3\mu$ . Conidia short, oblong, continuous,  $3.5$  to  $7\mu$ .

On unknown dicotyledonous plant.

Costa Rica: Experiencia Farm, July 18, 1923, 525.

When dry, the perithecia under the low power of the microscope appear like cups with a rod sticking upright in their centers. (Fig. 105.) This appearance is due to the infolding of the tops of the perithecia in drying.

This fungus combines the characters of both the Dothideales and the Sphaeriales. The prominent rostrum allies it with the Sphaeriales and perhaps most closely with the Coryneliaceae, though it does not appear really to belong in that family. The stroma is distinctly Dothideaceous in character, closely resembling the Dothideae (Figs. 37, 38). The very peculiar condition is frequently seen of isolated masses of stroma upon a perithecium. These may occur upon the top (Fig. 38) or elsewhere. They suggest that in earlier stages the perithecium is quite imbedded in a stroma and that as the stroma ages it flakes off leaving these remnants.

DOTHIDINA Theissen and Sydow

Ann. Myc., 13:302, 1915.

35. DOTHIDINA COSTARICENSIS Stevens n. sp.

[Figures 41-43]

Spot indefinite, yellow, long and narrow, often occupying the whole length of a leaf segment. Stromata about 1 mm. in diameter, black, amphigenous but more common above, very numerous, usually distinct, sometimes coalescing. At first subepidermal, later erumpent, the apex only emerging. Structure dothideoid. Locules usually solitary, globose, about  $370\mu$  broad,  $215$  to  $310\mu$  deep. Asci cylindrical, 8-spored,  $150 \times 14\mu$ . Paraphyses filiform, crooked. Spores at first hyaline, later brown, oval,  $14$  to  $18 \times 9\mu$ , usually uniseriate, occasionally inordinate.

On Palm (*Astrocaryum*, *Acrocomia* or *Bactria*)

Costa Rica: El Roble, July 25, 1923, 622.

This fungus clearly belongs to the Dothideae in the Dothideaceae rather than to the Scirrhineae in the Phyllachoraceae, though it indicates a transition form between these two families, in that the stroma has not the truly palisade character of the former family but is composed of cells more elliptical than rectangular. It also tends toward the latter family in that the emergence of the stroma above the epidermis is very slight, only the apex of the stroma protruding.

The species is quite distinct in several ways, notably so in the spore shape and size, from *D. palmicola* (Speg.) Theiss. and Syd. A very peculiar condition was observed in the asci which at maturity fall into eight segments, each of which contains one spore. (Fig. 43.) Before falling apart thus the ascus can be seen to be divided by septa, either transverse or oblique as need be to separate the spores from each other. Study of the asci of *D. palmicola* shows that in this species also the ascus falls into single-spored segments though asci with septa were not seen. De Bary<sup>35</sup> cites in the ascomycetes cases where the wall of the ascus forms a septum between each pair of spores though in the cases cited by him the spores fill the separated segments while in my species the spores do not do so. A similar condition of the asci is found also in *Othiella* (see page 46).

ACHORELLA Theissen and Sydow

Ann. Myc., 13:340, 1915.

36. ACHORELLA ATTALEAE Stevens n. sp.

Spot dead, 2 to 10 x 1 to 3 mm. oval to linear, black, yellow-bordered, hypophyllous, visible above as a yellowed discoloration. Stromata at first poorly developed, subepidermal, later erumpent, basal portion below the epidermis dothideoid, superficial part usually consisting of a unilocular, globose protuberance about 300 $\mu$  in diameter; rough walled; ten or more on one spot. Locule globose, about 340 $\mu$  in diameter. Base of the protuberance surrounded by a superficial crooked, nonhyphopodiate mycelium.

Asci 80 x 11 $\mu$ , 8-spored. Paraphyses filiform, slender, crooked, numerous; spores, yellow, 16 x 3.5 $\mu$ , obtuse, cylindrical, 1-septate, slightly constricted. Small pycnidial cavities about 100 to 150 $\mu$ , frequently occur on the loculiferous stroma.

On *Attalea cohune*.<sup>36</sup>

Panama: Gamboa, Aug. 16, 1923, 1079.

This fungus is distinctly parasitic, causing well defined diseased spots. The growth of superficial mycelium as well as the free perithecium-like protuberances gives to this fungus both the characters of the Dothids and of the Perisporiaceae though its closest relation is with the former. This species differs essentially from *A. ametableta* (Rehm.) Theiss. and Syd. from Brazil on *Baccharis* stems in the smaller stromata, smaller locules, in the shape of the spores and particularly in that the perithecial protuberances are often free on the stroma, not immersed in it as is the case in *A. ametableta*.

<sup>35</sup> Comp. Morph. and Biol. of the Fungi Mycetoza and Bacteria, Trans. by Garnsey, 1887:96.

<sup>36</sup> Det. by P. C. Standley.

37. *ACHORELLA COSTARICENSIS* Stevens n. sp.

[Figures 44, 45]

Spot none. Stromata epiphyllous, black, 1 to 2 mm. in diameter, much raised above the leaf surface, bearing numerous (10 to 30), globose perithecia on the stroma surface. Stroma centrally fastened, foot dothideoid. Locules globose, about  $150\mu$  in diameter. Asci 8-spored, conglobate. Spores brown, oblong, 1-septate,  $21$  to  $25 \times 10\mu$ . Paraphyses many, crooked, filiform, gelatinous. Conidial locules irregular in shape, conidia very minute, bacteria-like.

On *Mikania* sp.

Costa Rica: Cartago, Leg. Lancaster, July 24, 1923, 646 (type); Cartago, June 23, 1923, 57.

The hypostroma is quite remarkable in that it is made up of a coarse mycelium, hyaline when young but dark when old, that appears to be strictly if not entirely intercellular in character. The leaf, in the occupied region, is deformed to nearly three times its normal thickness. The stromata develop first in the mesophyll but soon become erumpent. This fungus rather closely resembles *A. guianensis* on the same genus of host, from British Guiana,<sup>37</sup> but is distinguished from it by the difference in the shape, size and constriction of the spores.

## PHYLLACHORACEAE

## TRABUTIINEAE

TRABUTIA Sacc. and Roum. emend Theiss. and Syd.

Rev. Myc., 3:27, 1881.

38. *TRABUTIA XYLOSMAE* Stevens n. sp.

[Figures 46, 106]

Stromata subcuticular, strictly epiphyllous, showing only from above, black, shining, raised, circular to irregular in shape, varying from minute ( $1\frac{1}{2}$  mm.) to 5 mm. in diameter. Thickly scattered over the leaf. Epidermal clypeus dense, black. Subepidermal stroma more loose. Ascigerous locules about 260 to  $500\mu$  wide, 110 to  $370\mu$  deep, several in a stroma. Paraphyses filiform, crooked. Asci 8-spored,  $144 \times 18\mu$ . Spores 1-celled, globose when young, globose to oval when mature,  $9\mu$  in diameter to  $9 \times 11$  to  $16\mu$ , usually uniseriate. Conidia filiform, about  $18\mu$  long, in cavities about  $180\mu$  wide or by coalescence much wider, and  $70\mu$  deep, borne on filiform conidiophores.

On *Xylosma salzmanni*.<sup>38</sup>

Costa Rica: El Alto, July 6, 1923, 243 (type); Cartago, July 2, 1923, 186.

<sup>37</sup> Stevens, F. L. Parasitic Fungi from British Guiana and Trinidad. Ill. Biol. Monog., 1924.

<sup>38</sup> Det. Standley.



On *Myroxylon ellipticum*.<sup>39</sup>

Costa Rica: La Palma, July 8, 1923, 276.

HYPOSTIGMA Sydow

Ann. Mycol., 23:337, 1925.

39. HYPOSTIGMA POLYADELPHA Sydow

Ann. Mycol., 23:337, 1925.

On *Buettneria aculeata*.<sup>40</sup>

Costa Rica: San Cecelia, Aug. 7, 1923, 748. Panama, Brazos Brook reservoir, Sept. 22, 1924, 736.

The fungus is quite unique in that the hyaline mycelium extends from stroma to stroma under the cuticle, usually one layer thick (Fig. 47), sometimes two layers (Fig. 47). Frequently it also extends downward between the epidermal cells (Fig. 52) and penetrates these cells, developing within rather extensive haustoria. The loculiferous mycelium always turns dark at the base of the locule; is flat and one cell thick, composed of cells that are approximately isodiametric. (Figs. 49, 51.) Over this floor is the arched covering (Fig. 50) which is also of isodiametric cells considerably darker than those of the base. The base extends outward at the margin in irregular projections, 3 to 7 $\mu$  long, but neither the base or the covering in any of its parts gives any indication of radiate structure. In age the whole covering of the locule breaks away leaving only the floor with a margin showing the attachment of the covering (Fig. 51). The position of this fungus is somewhat doubtful. In general character it resembles the Trabutiineae, near *Trabutiella*, but the stroma is so slightly developed that it is questionable whether any stroma should be recognized. The subcuticular development as well as the general appearance also suggest the Stigmataceae, but this fungus lacks entirely the radiate structure requisite to membership in that family. It is placed by Sydow in the Sphaeriaceae.

EURYACHORA Fuckel

Symb. Myc., 220, 1869.

40. EURYACHORA sp. ind.

On Unknown dicotyledonous plant.

Costa Rica: La Palma, July 8, 1923, 274; El Alto, July 6, 1923, 252.

SCIRRHINEAE

CATACOUA Theissen and Sydow

Ann. Myc., 12:280, 1914.

<sup>39</sup> Det. Maxon.

<sup>40</sup> Det. Standley.



41. *CATACOUA COSTARICENS* Stevens n. sp.

[Figure 108]

Spot irregular, slightly exceeding the stroma as a pale zone, yellow below. Stroma epiphyllous, subcuticular, black, flat or slightly raised, irregular in outline, 1 to 5 mm. across, about  $100\mu$  thick, filling the epidermis with an opaque, black layer about 11 to  $18\mu$  thick. The upper portion of the palisade layer is occupied by a similar layer. The part between these two layers is more thin-walled and less dark. Ascigerous locules 42 to  $56 \times 70$  to  $141\mu$  or  $78 \times 36\mu$ , located in the central layer of the stroma. Asci 4-8 spored, 21 to  $38 \times 7$  to  $10\mu$ . Paraphyses filiform, gelatinous. Spores  $14 \times 2$  to  $3\mu$ , hyaline, continuous, fusiform. Conidial locules 42 to  $56 \times 70$  to  $141\mu$  or  $78$  to  $436\mu$ , located in the central layer of the stroma. Conidia 5 to  $7 \times 1.2$  to  $1.7\mu$ . Conidiophores rod-shaped, simple, several times the length of the conidia.

On *Myrcia costaricensis*.<sup>41</sup>

Costa Rica: La Palma, July 8, 1923, 287.

This fungus differs essentially from all species of *Catacouma* described on the Myrtaceae. The conidial cavities are of especial interest.

42. *CATACOUA ZANTHOXYLI* Stevens n. sp.

[Figures 53, 54, 109, 110]

Spot subcircular, showing below as an indefinite, pale area. Stromata epiphyllous, black, punctiform, slightly raised, very many in each spot, the old ones toward the center, the younger toward the margin. Old stromata in the center of a spot are often denuded. Stromata develop in the epidermis and above the palisade. Epidermal clypeus black, about  $30\mu$  thick, up to  $540\mu$  across. Locules usually solitary, occasionally more than one, the locules then separated by dothideoid tissue, lenticular, up to  $460\mu$  wide,  $215\mu$  thick, floor hyaline. Asci basal, 8-spored. Spores hyaline, 1-celled, ovate,  $14$  to  $15\mu \times 8$  to  $9\mu$ , rounded at one end, pointed at the other. Paraphyses many, thin. Conidial locules also present, smaller than the ascigerous and bearing bacillar conidia.

On *Zanthoxylon* sp.<sup>42</sup>

Panama: Chagres, 3 miles from mouth, Aug. 23, 1923, 1290.

APIOSPORA Sacc.

Comp. gen. Pyren., 9, 1875.

43. *APIOSPORA STRIOLA* (Pass.) Sacc.

On Bamboo (*Chusquea pittieri* ?).

Panama: Tapia, Aug. 15, 1923, 1019.

<sup>41</sup> Det. Standley.

<sup>42</sup> Det. Standley.

The spores are very variable in size and it is really difficult to say which of the three species described on bamboo is here represented. It agrees, however, well with the one above named.

PHYLLACHORINEAE

PHYLLACHORA Nits.

Fuck. Symb. Myc., 216, 1869.

44. PHYLLACHORA AMBROSIAE (B. & C.) Sacc.

Syll. Fung., 2, 601.

[Figures 55, 56]

Spot brown, irregular, dead, definitely bordered, 0.5 to 2 cm. in diameter, bounded by a narrow yellow zone. Stromata barely visible above, but prominent below as rounded, black protuberances. Locules solitary in each stroma, but stromata occasionally contiguous, globose, 150 to 250 $\mu$  in diameter, ostiolate, asci basal, lower clypeus about 25 $\mu$  thick, locular wall about 11 $\mu$  thick. Stroma of the mesophyll loose, brown. Asci 8-spored, 90 to 110 x 11 $\mu$ . Spores uniseriate or inordinate, globose or short cylindrical, 11 to 14 x 7 to 11 $\mu$ , hyaline, 1-celled. Paraphyses filiform, long, crooked.

On *Podachaenium eminens*.<sup>43</sup>

Costa Rica: Peralta, July 13, 1923, 467.

The stroma in the upper leaf surface occasionally develops to fill the region between the epidermis and the locule, thus emphasizing the Dothid relationship.

45. PHYLLACHORA ANTHEPHORAE Syd.

Ann. Myc., 13:39, 1915.

On *Antheophora hermaphrodita*.<sup>44</sup>

Costa Rica: Swamp Mouth, Aug. 8, 1923, 774.

This specimen appears to agree in all particulars with the description by Sydow drawn from the type collected in Jamaica.

46. PHYLLACHORA CASIMIROAE Stevens and King n. sp.

[Figures 57, 58, 111]

Stromata extending through the leaf. Clypei epidermal, black, irregular, confluent with stroma; on the upper surface slightly raised, shiny and frequently minutely pimpled; on lower surface prominent, lustrous, but sometimes appearing hairy because of adhering trichomes, bearing one to several broadly conical projections at the apices of which the ostioles form; diameter 3 mm. or more below, smaller above; thickness 20 to 40 $\mu$ .

<sup>43</sup> Det. Standley.

<sup>44</sup> Det. Chase.

Ostiole about  $80\mu$  across. Locules solitary or several (1 to 12), typically oval,  $520\mu$  wide,  $400\mu$  deep, asci and paraphyses numerous and covering all of interior except near the ostiole; lined by a layer of hyaline mycelium which is covered by and structurally continuous with a dark mycelial layer. Asci nearly cylindrical, hyaline, thin walled, 4 to 8 spored (usually 8), apex somewhat truncate,  $16$  to  $21\mu$  x  $144$  to  $168\mu$ . Paraphyses filiform, up to  $254\mu$  long, hyaline. Spores one-celled, hyaline or slightly grayish, fusoid,  $12$  x  $28\mu$ .

On *Casimiroa tetrameria*.

Costa Rica: El Alto, July 6, 1923, 233, 234.

This species of *Phyllachora* is unique in showing all of the generic structural characteristics, but in addition having a dark mycelial layer surrounding the hyaline mycelial layer from which the asci arise (Fig. 57). There is direct organic connection between these layers, the same mycelial strand appearing dark and dense in the one and hyaline in the other. The large size of the stroma and abundance of frail thin-walled asci are unusual.

#### 47. PHYLLACHORA CHAETOCLOAE Stevens

Ill. Biol. Monogs., 8:184, 1923.

On *Chaetochloa vulpiseta*.<sup>45</sup>

Panama: Gamboa, Aug. 16, 1923, 1078.

On *Pennisetum distachyum*.<sup>45</sup>

Costa Rica: San Vicente del Coronado, June 30, 1923, 174.

On *Paspalum fasciculatum*.

Costa Rica: Sabrio, Aug. 8, 1923, 809.

#### 48. PHYLLACHORA CHUSQUEAE P. Henn. and Lind.

Hedw., 36:224, 1897.

On *Chusquea pittieri*.<sup>46</sup>

Panama: Alehjuela, Aug. 18, 1923, 1122; Juan Mina, Aug. 18, 1923, 1165.

#### 49. PHYLLACHORA DIOCLEAE P. Henn.

Hedw., 43:252, 1904.

On *Dioclea reflexa*.<sup>47</sup>

Costa Rica: Port Limon, Aug. 10, 1923, 876.

This specimen agrees well with the original description given by P. Hennings as drawn from material collected by Ule in the Amazon region. The description given by Theissen and Sydow<sup>48</sup> differs somewhat from the original description in several details, particularly as to the size of the

<sup>45</sup> Det. Mrs. Chase.

<sup>46</sup> Det. Standley.

<sup>47</sup> Det. Blake.

<sup>48</sup> l. c.

stromata and of the spores, giving the spores as markedly larger than in the original description, (20 to 23 x 6 $\mu$  as against 18 to 22 x 4 to 5 $\mu$ ).

50. *PHYLLACHORA ENGLERI* Speg.

Fung. Guaranit., I. no. 267.

On *Anthurium aemulum*.<sup>49</sup>

Costa Rica: Siquirres, July 31, 1923, 708.

On *Anthurium* sp.

Costa Rica: Peralta, July 12, 1923, 404; Cachi (4500 ft. alt. Leg.

C. H. Lankester) Aug. 5, 1923, 739.

51. *PHYLLACHORA ICACOREAE* Stevens n. sp.

[Figures 59, 112]

Spot none or consisting only of a slight bleaching of the tissue surrounding the stromata. Stromata, circular when mature, usually about 3 mm. in diameter; above black and shining, slightly arched; below black, dull, slightly arched. Upper and lower clypeus well developed in the epidermis, about 18 to 25 $\mu$  thick, densely black. Stroma of the mesophyll poorly developed, consisting mostly of a loose network. Locular wall well defined, dense, brown, about 18 $\mu$  thick. Locules subglobose, located in the mesophyll, opening epiphyllous, about 170 to 230 $\mu$  in diameter. Paraphyses filiform, numerous, Asci about 90 to 100 x 7 $\mu$ . Spores oval, oblong, 1-celled, hyaline, 11 x 5 $\mu$ .

On *Ikacorea* sp.<sup>50</sup>

Costa Rica: Cartago, June 23, 1923, 46 (type) 72, 89.

Three species of *Phyllachora* are recorded by Theissen and Sydow,<sup>52</sup> as on the Myrsinaceae. Of these *P. pittieri* Theiss. and Sydow on Myrsine has much larger spores; *P. sinik-lagaraik* Speg. on Myrsine, has spores only somewhat thicker but is clearly set apart by its small stromata, each with few locules; *P. ardisiae* P. Henn. on Ardisia by the shape of the stromata.

52. *PHYLLACHORA JURAENSIS* P. Henn. var *minima* Stevens n. var.

Characters as in the species except as follows: Asci 80 to 144 $\mu$  long. Spores oblong, obtuse, often slightly pointed at one end, continuous, hyaline, 14 to 18 x 3.5 $\mu$ .

On *Brownea* sp.

Panama: Tapia, Aug. 15, 1923, 1025.

The species was originally described by Hennings<sup>51</sup> on *Brownia* sp. from the Amazon and is also listed and described by Theissen and Sydow.<sup>52</sup> These two descriptions differ somewhat as to spore and ascus measurements, but both give asci much shorter than the dimensions given above, and both give spores much larger than those given above; 20 to 26 x 5 to 6 $\mu$  in Hennings; 22 to 28 x 4.5 to 5.5 $\mu$  by Theissen and Sydow.

<sup>49</sup> Det. S. F. Blake.

<sup>50</sup> Det. Standley.



## 53. PHYLLACHORA LACTEA Theiss. and Syd.

Ann. Myc., 13:497, 1915.

On *Cassia* sp.

Costa Rica: Columbiana, July 19, 1923, 568; Siquirres, Aug. 1, 1923, 724.

Among the fifty and more species of *Phyllachora* recorded on legumes there are many with punctiform, unilocular stromata, and many of these agree quite closely in spore size and in other characters.

Two species are described on *Cassia*. Namely *P. cassiae* P. Henn and *P. bakeriana* P. Henn. The present species differs from both of these in several ways. It does, however, appear to agree sufficiently well with the above named species to warrant reporting it under that name. My own notes on the characters shown by my specimen are as follows: spot indefinite, irregular, poorly defined, containing numerous stromata which are punctiform, unilocular, ostiolate, 170 to 215 $\mu$  broad and deep. Upper clypeus consisting of a thickening and darkening of the upper part of the locular border, less broad than the perithecial diameter; basal stroma absent. Asci 97 x 18 $\mu$ . Paraphyses filiform. Spores oval, 14 to 18 x 7 $\mu$ , hyaline.

## 54. PHYLLACHORA LITSEAE Koord.

Bot. Unt. ü einige in Java vorkommende Pilze 181, Verh. Kon. Akad. Wet. Amsterdam, II Sect., Deel 13, no. 4, 1907.

On *Nectandra glabrescens*.<sup>53</sup>

Panama: Tapia, Aug. 15, 1923, 1017.

## 55. PHYLLACHORA MAYDIS Maub.

Bull. Soc. Myc. Fr., 20:72, 1904.

On *Zea mays*.

Panama: Gamboa, Aug. 17, 1923, 1106.

## 56. PHYLLACHORA MEIBOMIAE Stevens n. sp.

[Figures 60, 113]

Spot none. Stromata epiphyllous, not visible from below, black, irregular in outline, 1 to 2 mm. in diameter, showing 1 to several ostioles. Epidermal clypeus black, broadly extending, about 18 to 25 $\mu$  thick, subepidermal stroma brown, dothideoid, mostly limited to the interocular region. Locules one to few in each stroma, 170 to 246 $\mu$  wide, 107 to 140 $\mu$  deep, bounded by a brown wall 7 to 14 $\mu$  thick. Asci borne basally, 8-spored,

<sup>51</sup> Hedw., 43:252. 1904.

<sup>52</sup> Theissen and Sydow l. c.

<sup>53</sup> Det. Standley.



64 to 90 x 10 to 14 $\mu$ , stipitate. Spores oblique or conglobate. Paraphyses filiform, crooked. Spores hyaline, continuous, 18 x 3.5 $\mu$ .

On *Meibomia* sp.

Costa Rica: San Cecelia, Aug. 7, 1923, 756 (type) and 745.

The black epidermal clypeus with but scant stromatic development below is quite characteristic. The stromata on the two specimens, which are of two distinct species of *Meibomia*, are somewhat different in appearance but the spore characters are the same.

57. *PHYLLACHORA OCTEICOLA* Stevens and Dalby

Bot. Gaz., 68:57, 1919.

*PHYLLACHORA OCOTEICOLA* var. *COSTARICENSIS* Stevens n. var.

Though resembling *P. ocoteicola* somewhat in stroma and spore<sup>54</sup> this variety differs markedly in that the stromata are black and shining above and distinctly raised and show the impression of the loculi, while *P. ocoteicola* differs in all these regards, being flat and dull above. The stromata in this variety are also less angular, more nearly circular.

On *Ocotea*<sup>55</sup> sp.

Costa Rica: Peralta, July 12, 1923, 390.

58. *PHYLLACHORA OPLISMENI* Syd.

Ann. Myc., 5:339, 1907.

On *Oplismenus burmanni*.<sup>56</sup>

Costa Rica: Siquirres, Aug. 1, 1923, 728.

This appears to agree completely with the description by Sydow and therefore with the specimen collected by Tonduz (no. 188) in Costa Rica.

59. *PHYLLACHORA PANAMENSIS* Stevens n. sp.

Spot indefinite, consisting of a pale or yellowish region 3 to 4 mm. wide surrounding the stromata. Stromata numerous, scattered, somewhat irregular in shape, 1 to 1.5 mm. in diameter, visible from both sides of the leaf; above shining, black, slightly raised; below, slightly raised, dull, showing the locules clearly. Upper and lower clypeus each epidermal and about 30 $\mu$  thick. Upper clypeus extending slightly beyond the locules. Stroma in the mesophyll scant, usually consisting of merely a slight, loosely woven, mass between the locules. Locules 150 to 260 $\mu$  deep, 150 to 300 $\mu$  wide, opening epiphyllous. Asci mainly, basal. Paraphyses filiform, numerous, crooked, asci 87 x 7 $\mu$ , long, narrow. Spores uniseriate or oblique, long, oval, 14 x 6 to 7 $\mu$ , thickest in the middle.

<sup>54</sup> The original description errs in the spore measurement through the omission of a decimal point. The description should read 17x5.4 to 7 $\mu$ .

<sup>55</sup> Det. Standley.

<sup>56</sup> Det. Chase.

On *Rourea glabra*.<sup>57</sup>

Panama: Gamboa, Aug. 16, 1923, 1094; Juan Mina, Aug. 18, 1923, 1351.

60. PHYLLACHORA PASPALICOLA P. Henn.

Hedw., 48:106, 1908, Rehm Ascom. 1785.

On *Paspalum conjugatum*.

Costa Rica: Peralta, July 11, 1923, 335a; July 13, 1923, 435a; July 13, 1923, 815a.

61. PHYLLACHORA PICRAMNIAE Stevens n. sp.

[Figures 61, 62, 121]

Spots circular, indefinite bordered, yellow, surrounding the stromata by a zone about 3 mm. wide. Stromata circular, raised, both surfaces black and shining, about 3 mm. in diameter. Stromata in each epidermis dense and black, in the mesophyll much less dense. Locules in one row, opening epiphyllous, globose or somewhat flattened, 185 to 246 $\mu$  broad, 150 to 231 $\mu$  deep. Asci cylindrical, short stalked, 93 x 11 $\mu$ , spores oblique. Paraphyses filiform, gelatinous, numerous. Spores continuous, hyaline, 21 to 25 x 5 $\mu$ , oblong, tapering slightly from middle to each end.

On *Picramnia bonplandiana*.<sup>58</sup>

Costa Rica: Aserri, June 26, 1923, 119 (type); Desamparados, June 27, 1923, 138.

Only one *Phyllachora* appears to be recorded on the Simarubaceae and that quite different from the one above described. *Phyllachora roureae* Syd. was described from the conidial stage only on *Rourea erecta* from the Philippines<sup>59</sup> and later was excluded from the genus *Phyllachora* by Theissen and Sydow<sup>60</sup> because of the lack of description of asci and spores. It in some respects resembles this species. Our specimens show no conidia. The present species differs markedly in spore shape and size from *P. connari* Syd. and *P. connarina* Rac. also on members of the Connaraceae.

On *Picramnia antidesma*.<sup>61</sup>

Costa Rica: El Alta, July 6, 1923, 242.

The specimens on the last named host differ markedly from those on the other host as follows: The stromata are much less abundant, much smaller, and are dull rather than shining. The locules are usually much smaller, 125 to 218 $\mu$  broad, thus occupying much less space in the mesophyll. The spores on the two hosts however, measure the same. This

<sup>57</sup> Det. Standley.

<sup>58</sup> Det. Standley.

<sup>59</sup> Sydow, H. & P. Enumeration of Philippine fungi, with notes and descriptions of new species. Phil. Jour. Sc. C. Bot., 8:247, 1913.

<sup>60</sup> Die Dothideales. Ann. Myc., 13:575, 1915.

<sup>61</sup> Det. Standley.

makes an interesting case of a fungus occurring on two separate hosts and showing quite different morphology on the two. Whether this difference is due to alteration of the fungus or to differences in the host reaction is unknown. That the fungi on the two hosts are closely related, cospecific, is probable from the appearance of the spores and the general structure of a stroma.

62. *PHYLLACHORA SAPINDACEARUM* Stevens n. sp.

Spots yellow to brown, dead, circular, indefinite, about 5 mm. in diameter, with one stroma at the center, visible from both sides of the leaf. Stromata about 1 mm. in diameter, black and shining above, dull black below. Clypei, above and below, each about 30 to  $45\mu$  thick, epidermal, densely black. Mesostroma pale, scant. Locules 60 to  $140\mu$  deep, 120 to  $340\mu$  wide, surrounded by a definite dark border, few in a stroma, usually one. Asci 8-spored, inordinate,  $70 \times 11\mu$ , basal. Paraphyses numerous, filiform. Spores oblong,  $11 \times 7\mu$ , continuous, hyaline.

On *Serjania mexicana*.

Panama: France Field, Aug. 24, 1923, 1327.

This differs essentially from *P. duplex* Rehm on *Serjania* from Brazil, also from *P. subrepens* Speg., and *P. insueta* Sydow in spore shape and size.

63. *PHYLLACHORA STEVENSII* Sydow n. sp.

[Fig. 115]

Spot vague, indefinite, slightly discolored, 3 to 8 mm. in diameter, visible below as a slightly pale region. Stromata epiphyllous, black, shiny, punctiform, 150 to  $180\mu$  in diameter, numerous in irregularly arranged groups. Clypeus in the epidermal cells, about  $15\mu$  thick, dense, extending barely to the diameter of the locule. Stroma development at the base of the locule limited to a small black shield, much smaller than the superior clypeus. Locules 107 to  $185\mu$  in diameter, 46 to  $90\mu$  deep. Paraphyses numerous, short and thick, 0.75 to  $1\mu$ . Asci 50 to  $57 \times 7$  to  $18\mu$ , 8-spored. Spores oval, hyaline to green,  $8 \times 5\mu$ . Locule 154 to  $215\mu$  broad, 140 to  $185\mu$  deep.

On *Meibomia* sp.

Panama: Gamboa, Aug. 17, 1923, 1007 (type); Gatuncillo, Aug. 18, 1923, 1150.

The type of stroma in this fungus is much like that of *P. inclusa* as described and figured by Theissen and Syd. (Ann. Myc., 13, Taf. 3. fig. 14), and is similar also to *P. calervaria* (Taf. 4 fig. 5).

In specimen No. 1150 the spores are a trifle larger and the clypeus extends somewhat further to each side of the locule. This species is much like *P. ramosii*, (P. Henn.) Theiss. and Syd. but differs from it in its much more highly developed stroma.

64. *PHYLLACHORA TRAGIAE* (Berk and Curt) Sacc.

Syll Fung. 2. 601.

On *Croton* sp.

Costa Rica: Escasu, June 29, 1923, 159.

The epidermal cells are densely crowded with dark mycelium forming the epidermal clypeus. Below this is a thick layer of somewhat less dense stroma, while between this and the palisade layer is another stromatic layer that is comparatively loose and light-colored.

The conidial locules are borne in the upper, dense, dark region of the stroma immediately below the epidermal clypeus, while the ascigerous locules are found deeper down, below the dense layer of stroma and in the more loose layer.

On *Croton glaucescens*.<sup>62</sup>

Panama: France Field, Aug. 24, 1923, 1322; Juan Diaz, Aug. 21, 1923, 1226; Tapia, Aug. 15, 1923, 1011.

The specimens on the last mentioned host differ somewhat in the shape of the locules and the stromata; but this may well be due to the difference in the host tissue.

65. *PHYLLACHORA TROPHIS* Stevens, n. sp.

[Figs. 63-65]

Spot small, circular, indefinite, consisting of a pale zone surrounding the stromata, visible from both sides of the leaf. Stromata solitary in each spot, about 1 mm. in diameter, black and shining above, flat or slightly raised; below dull black. Stromatic development in the upper and lower epidermis scant, usually only a few cells being filled with black mycelium. A layer of black, dense stroma about  $36\mu$  thick usually develops under each epidermis, while the mesophyll layer between these two regions is with but scant, and hyaline, mycelium. Locule in the mesophyll, flattened, about  $380\mu$  in diameter, 80 to  $90\mu$  deep, bounded by a thin, hyaline border, opening epiphyllous. Asci basal, 8-spored, 72 to  $90 \times 7$  to  $11\mu$ . Spores oval, 9 to  $12 \times 7$  to  $8\mu$ , 1-celled, hyaline. Paraphyses filiform, crooked.

On *Trophis racemosa*.<sup>62</sup>

Costa Rica: Cartago, June 23, 1923, 85.

This *Phyllachora* is remarkable chiefly for the scant epidermal stromata with black bands of subepidermal stromata, and with a hyaline region in the mesophyll between these. On the same leaves occurs a conidial stroma, Dothideaceous in character, but so different in stroma from this *Phyllachora* that it is difficult to regard them as being the same. With both of these stromata the leaf is enlarged to about twice its normal thickness.

The conidial stroma may be described as follows:

Upper clypeus weakly developed, limited to the epidermal cells, which are but partly filled with mycelium; lower epidermal clypeus still more

<sup>62</sup> Det. Standley.



scant, some of the cells being devoid of mycelium. Mesophyll well packed with a brown stroma. Locule usually solitary, opening epiphyllous. Conidial locules opening epiphyllous, in the middle of the mesophyll, 40–180 $\mu$  in diameter. Conidia 1-celled, oblong, yellow, 73.5 $\mu$ . Conidiophores simple, filiform, 14 to 20 $\mu$  long, 3 $\mu$  thick.

66. *PHYLLACHORA ULEI* Wint.

Grevillea, 15:90, 1886.

On *Dioscorea* sp.

Costa Rica: Limon, Aug. 7, 1923, 772; Sabario, Aug. 8, 1923, 798; Port Limon, Aug. 10, 1923, 875.

Panama: Panama, Aug. 14, 1923, 1003; Tapia, Aug. 15, 1923, 1006; Gamboa, Aug. 16, 1923, 1083; Pedro Miguel, Aug. 16, 1923, 1101; Alehjuela, Aug. 18, 1923, 1128; Gatuncillo, Aug. 18, 1923, 1144; Frijoles, Aug. 20, 1923, 1183; Panama, Aug. 21, 1923, 1216; Juan Diaz, Aug. 21, 1923, 1243.

67. *PHYLLACHORA VISMIAE* Stevens n. sp.

Spot yellow, irregular, about 3 to 5 mm. in diameter, border indefinite, Stroma black, irregular in outline, about 2 mm. in diameter. Spot visible only from above, stroma faintly showing below. Black epidermal clypeus present above and below, extending far beyond the locules, development in the mesophyll scant. Locules one to several in each stroma, 150 to 330 $\mu$  in diameter, 140 to 231 $\mu$  deep, border brown. Asci basal, long, cylindrical, 112 x 11 $\mu$ ; spores uniseriate, oblique. Paraphyses filiform. Spores oblong, 12 to 18 x 7 $\mu$ .

On *Vismia guianensis*.<sup>63</sup>

Costa Rica: Escasu, July 29, 1923, 155.

No *Phyllachora* has heretofore been described on any member of the Guttiferae and the only *Dothid* recorded is an *Endodothella* on *Vismia* from Costa Rica.

68. *PHYLLACHORA* sp. indet.

On unknown dicotyledonous plant.

Panama: Juan Diaz, Aug. 21, 1923, 1255. This specimen though undeterminable has been considered by Blain<sup>64</sup> on account of its interesting morphology.

*PHYLLACHORELLA* Syd.

Ann. Myc., 12:489, 1914.

<sup>63</sup> Det. Standley.

<sup>64</sup> Blain, W. L. Mycol. 29:1, 20. 1927.



69. *PHYLLACHORELLA SCHISTOCARPHAE* Stevens n. sp.

[Figures 66, 116]

Spots indefinite, of irregular shape, pale yellow, 1–2 cm. in diameter, visible above and below. Stromata punctiform, numerous and irregularly grouped in the spots, black above and slightly raised. Stroma limited to a very slight epidermal clypeus, with sometimes a scant stromatic development between the locule and epidermis. Ostiole well developed. Locule in the mesophyll, globular, 140 to 310 $\mu$  in diameter, bounding layer about 45 $\mu$  thick, hyaline, asci borne basally. Asci 8-spored, aparaphysate. Spores hyaline, irregularly oval, 1-celled, 11 to 14  $\times$  5.5 $\mu$ , somewhat thicker in the middle than at the ends.

On *Schistocarpha hoffmanii*.<sup>65</sup>

Costa Rica: Peralta, July 13, 1923, 434, 454.

This fungus with its thin hyaline locular wall, and well defined ostiole would doubtless by many be classified as one of the Sphaeriaceae, and placed in the genus *Laestadia*. It has, however, always the rudiments of an epidermal clypeus and quite often also a slight subepidermal stromatic development, which appear to me to place it with those uniloculate *Phyllachoras* which have but small clypei, this specimen representing an extreme reduction. The absence of paraphyses places it in *Phyllachorella* rather than *Phyllachora*.

## SPHAERODOTHIS Shear

Mycol., 1, 162, 1909.

70. *SPHAERODOTHIS CIRCUMSCRIPTA* (Berk.) Theiss. and Syd.

Ann. Myc., 13:579, 1915.

On *Sophoelesia* sp.<sup>66</sup>

Costa Rica: Cartago, June 23, 1923, 41 and 60.

The material of this species is scant and spores few. While I find no dark spores and ought perhaps therefore to place the fungus in *Phyllachora*, still it appears to agree so well with the above named fungus that I venture to so report it. The long, narrow, pointed spores are quite characteristic, as is also the peculiarly limited stroma.

71. *SPHAERODOTHIS SCLERIAE* (Rehm) Stevens n. comb.

*Phyllachora scleriae* Rehm, Hedw., 39:232, 1900.

On *Scleria melaleuca*.<sup>67</sup>

Costa Rica: Peralta, July 13, 1923, 419, July 11, 1923, 317; Port Limon, Aug. 10, 1923, 871.

On Sedge.

<sup>65</sup> Det. Standley.

<sup>66</sup> Det. Maxon.

<sup>67</sup> Det. Standley.

Costa Rica: Peralta, July 12, 1923, 907.

On *Scleria pterota*.<sup>67</sup>

Costa Rica: Port Limon, Aug. 9, 1923, 825.

The species was originally described as on "*Scleria* sps" from Brazil. The shape of the spores—fusiform, pointed at each end with one end slightly thicker than the other—is very characteristic; so definitely so as to leave no doubt that the present specimens are co-specific with *Phyllachora scleriae*. The ascospores when fully mature are brown, necessitating change in the generic name. Mature brown spores are only rarely seen. They differ slightly from the immature spores in that they are less pointed but the transition from the younger pointed shape to the older obtuse form is clearly traceable in a single locule.

72. *SPHAERODOTHIS SPHAEROSPERMA* (Winter) Stevens and Moore n. comb.

*Phyllachora sphaerosperma* Winter, Hedw., 23:170, 1884; Syll. Fung. 9:1027.

On *Cenchrus viridis*.

Costa Rica: Peralta, Aug. 1, 1923, 736; Swamp Mouth, Aug. 8, 1923, 775.

Panama: Gamboa, Aug. 17, 1923, 1116.

This specimen agrees in every detail with the type specimen of *Phyllachora sphaerosperma* Winter, issued by Rabenhorst in "*Fungi Europaei*" no. 3062 except that occasional spores were found in ours which were distinctly brown. In both however numerous spores of a smoky gray tinge appear. Theissen and Sydow<sup>68</sup> describe the spores as elliptical, 11 to 12 by 6.5 to 7 $\mu$ . In both the type and in our specimen the spores are globose or subglobose, commonly 10 $\mu$  in diameter but ranging from 8 to 12 $\mu$ . This agrees with Rabenhorst's description accompanying the type specimen and with Saccardo.<sup>69</sup> Saccardo also notes the dark spores and suggests *Auerswaldia* as the genus. The occurrence of the brown spores leads to the formation of this new combination.

PHAEODOTHIS Syd.

Ann. Myc., 2:166, 1904.

73. *PHAEODOTHIS COSTARICENSIS* Stevens n. sp.

[Figures 67, 68]

Spot none. Stromata scattered, strictly hypophyllous, subcircular, about 1 mm. in diameter, developed as a dense, dark clypeus, subtended by a more loose, less dark stroma reaching into the mesophyll, but rarely extending to more than half way through the leaf. Locules few in each

<sup>68</sup> Theissen and Sydow. Ann. Myc., 13:445.

<sup>69</sup> Saccardo, Sylloge Fungorum, 9:1027.

stroma (usually 1 to 5). Asci 8-spored, long, narrow,  $90 \times 7\mu$ . Paraphyses filamentous. Spores yellow, uniseriate, oval, 10 to  $11 \times 3$  to  $4\mu$ , 1-septate, slightly constricted, pointed at each end. Conidial locules irregularly globose or flattened, usually developed in the mesophyll, external to the dark stroma, each locule surrounded by a delicate, hyaline wall. Conidia very numerous, oval, yellow,  $7 \times 2\mu$ .

On unknown member of the Rubiaceae.

Costa Rica: Siquirres, July 31, 1923, 673.

Only eight species of this genus are given by Theissen and Sydow. Conidia are mentioned for none. All differ essentially from our species.

PHRAGMOCARPELLA Theissen and Sydow

Ann. Myc., 13:601, 1915.

74. PHRAGMOCARPELLA PUIGGARII (Speg.) Theiss. and Syd.

Ann. Myc., 13:601, 1915.

On *Oplismenus burmanni*.

Costa Rica: San Cecelia, Aug. 7, 1923, 755.

OPHIODOTHELLA v. Höhn.

Fragn., 12: no. 630, 1910.

75. OPHIODOTHELLA PANAMENSIS Stevens n. sp.

[Figures 69-71]

Spots up to about 5 mm. in diameter or by coalescence larger, irregularly circular, bordered by a narrow yellow line, each occupied by one stroma. Stromata about 1 to 2 mm. in diameter, visible from both leaf surfaces, dull black, rough. Epidermal, black clypeus present both above and below, accompanied by the development of a dark subepidermal stroma about 70 to  $110\mu$  thick on the upper side. Major portion of the stroma below the palisade layer, colorless, thin walled prosenchymatic, about  $230\mu$  thick and 700 to  $900\mu$  in diameter, extending also to some extent between the palisade cells and developing extensively between the cells of the spongy parenchyma. Locules several in each stroma, located in the hyaline stroma of the mesophyll, globose, about  $230\mu$  in diameter, developing an ostiole which becomes somewhat rostrate, opening hypophyllous. Asci long, narrow,  $72 \times 7\mu$ , stalked, arising from all parts of the locule border. Spores filiform, curved, 61 to  $65 \times 1.5\mu$ , obtuse, hyaline. Paraphyses none.

On *Cordia heterophylla*.<sup>70</sup>

Panama: Panama, Aug. 21, 1923, 1217; Juan Mina, Aug. 18, 1923, 1163.

This fungus is remarkable in several ways chiefly as follows: 1. Its most extensive stromatic development is below the palisade layer. This

<sup>70</sup> Det. Standley.

character is seen in very few fungi. Logically the definite location of the stroma below the palisade layer is just as significant as to find it definitely subcuticular or subepidermal, characters on which Sydow and Theissen base their *Trabutiineae*, *Schirrhiineae* and *Phyllachorineae*. This species might therefore be considered as representing a fourth and coordinate group. 2. The loculiferous stroma is pale, hyaline, yet it has the typical palisade arrangement of cells characteristic of the *Dothideaceae*. This is an extremely rare condition. It is approached in *Anisochora* and is suggested by certain fungi of the *Clavicipiteae* related to *Dothichloe*. 3. The ostiolar development is much more suggestive of the *Sphaeriales* than of the *Dothideales*, in fact, is such that the inclusion of this form in the *Dothideales* is perhaps rendered questionable. 4. The occurrence of filiform spores in the *Dothideales* is far from common. Theissen and Sydow give only four genera with filiform spores. 5. This fungus shows much similarity with *Scolecodothopsis ingae*, particularly in the location of the stroma below the palisade layer, but the two differ in that the present form possesses a highly developed stroma while *S. ingae* has a very poorly developed stroma.

#### MONTAGNELLACEAE

##### HAPLOTHECIUM Theissen and Sydow

Ann. Myc., 13:614, 1915.

##### 76. HAPLOTHECIUM DIOSCOREAE Stevens n. sp.

[Figure 72]

Spot circular, 2 to 5 mm. in diameter, tan-colored, visible from both leaf surfaces, border indefinite. Stromata visible only from below, punctiform, dull black. Locules inordinate, subglobose, 125 to 200 $\mu$  in diameter, border dark, about 15 $\mu$  thick. A black clypeus, 20 to 25 $\mu$  thick, is present over some of the locules. Extralocular stroma hyaline, loose. Paraphyses numerous, filiform, gelatinous. Asci 90 x 11 $\mu$ . Spores 14 to 18 x 7 to 8 $\mu$  elliptical.

. On *Dioscorea* sp.

Costa Rica: Peralta, July 14, 1923, 475.

The asci and spores of this fungus are very similar to those of *Phyllachora ulei*, but the stroma is entirely different.

#### DOTHIDEALES IMPERFECTI

##### PYCNIDIOSTROMA Stevens n. gen.

Stroma of the *Phyllachorineae*; conidia hyaline, continuous, oval or fusiform.



77. *PYCNIDIOSTROMA EUGENIAE* Stevens n. sp.

[Figures 73, 117, 118]

Stromata black, subcircular, extending through the leaf, 3 to 6 mm. in diameter, margin sharply defined, raised; pycnidial locules visible from the upper surface, disposed in one row close to the circumference of the stroma. Upper and lower clypei limited to the epidermis, dark, mesostroma pale, loose. Pycnidial locules lenticular, 90 to 230 $\mu$  broad, about 80 $\mu$  deep, border hyaline, hymenium lining whole of periphery, including the top, no ostiole. Conidiophores hyaline, filiform, simple, about 7 to 10 $\mu$  long. Conidia hyaline, 1-celled, oval to fusiform, 7 x 2 $\mu$ .

On *Eugenia oerstediana*.<sup>71</sup>

Costa Rica: Cartago, July 2, 1923, 187 (type); El Alto, July 6, 1923, 224.

On *Calyptranthes costaricensis*.<sup>71</sup>

Costa Rica: El Alto, July 6, 1923, 237, 250.

The most characteristic features of this fungus are the circular arrangement of the locules, the definite raised border of the stroma, and the loose hyaline mesophyll.

## SPHAERIALES

## CUCURBITARIACEAE

## OTTHIELLA Sacc.

Syll. Fung., 1:739. (as subgenus).

78. *OTTHIELLA FOURCROYAE* Stevens and De Coursey n. sp.

[Figures 74, 119]

Perithecia cespitose, erumpent, superficial, carbonaceous, globose, 250 $\mu$  in diam., without stroma. Asci cylindrical, eight-spored, stipitate, 120 to 125 x 28 to 32 $\mu$ , apophysate; spores elliptical, hyaline or slightly tinted, 1-septate, constricted, 22 to 24 x 6 to 8 $\mu$ .

On *Fourcroya* sp.

Costa Rica: El Alto, July 6, 1923, 251.

It was considered advisable to distinguish between *Otthiella ribis* Tracy and Earle and this species on the basis of the wide generic separation of the hosts and considerable difference in spore measurements, though the description of *Otthiella ribis* is so general that it might be made to include this species.

Attention is called to the asci which are apparently, clearly cross-walled. See Fig. 74. This unusual occurrence has also been observed by Stevens in *Dothidina costaricensis*, see page 29.

Asci showing much the same general appearance as these are figured by Julius Klein<sup>72</sup> as occurring in *Ascobolus elegans* with the comment

<sup>71</sup> Det. Standley.

<sup>72</sup> Verhandl. d. k. k. zool. Bot. Ges., 20.: 1870. Taf. 10, fig. 19.



“Die Sporen werden gleich nach ihrer Bildung und auch im reifen Zustande einzeln von einer farblosen Hülle umgeben, mit der sie unter einander zusammenhängen (Taf. X, fig. 19). Wie bekannt, werden die reifen Sporen, indem die Asci sich oben deckelartig öffnen, aus denselben herausgespritzt, und finden sich meist auch noch nachher durch ihre Hüllen miteinander verbunden.”

## CORYNELIACEAE

## CORYNELIA Fries ex Acharius

Syst. Myc., 2:535, 1822.

## 79. CORYNELIA sps.

On *Podocarpus* sp.

Costa Rica: Cartago, June 23, 1923, 47.

Owing to the condition of the material the asci and spores could not be found. The apices of the perithecia were found to be 2 to 4 lobed, though the stromata closely resemble those of *C. portoricensis* Fitz.

## MYCOSPHAERELLACEAE

## MYCOSPHAERELLA Johans.

Svamper fran Island.

## 80. MYCOSPHAERELLA CASSIAE Stevens n. sp.

Spots subcircular, 3 to 7 mm. in diameter, brown to black, concentrically marked with dark lines, border definite. Perithecia numerous, hypophyllous, immersed, brown, very minute, 36 to 43 $\mu$  in diameter, slightly rostrate, ostiolate, reticulate. Mycelium dark, coarse. Asci 8-spored, 29 x 11 $\mu$ , paraphysate. Spores inordinate, 2-celled, hyaline, oblong, 4 x 0.5 $\mu$ .

On *Cassia* sp.

Costa Rica: Columbiana, July 19, 1923; 909; Siquirres, Aug. 1, 1923, 724.

The spores and perithecia are very much smaller than those of *M. sordidula* Speg., also on *Cassia*.

## 81. MYCOSPHAERELLA PLANTAGINICOLA (Pat.)

*Sphaerella plantaginicola* Pat. Bull. Soc. Myc. d. Fr., 9:153, 1893.

On *Plantago hirtella*.<sup>73</sup>

Costa Rica: La Palma, July 8, 1923, 293; Cartago, June 23, 1923, 38; El Alto, July 6, 1923, 253 and 241.

These specimens agree well with the descriptions of the above named species and differ decidedly from *M. plantaginis* Sollm., which has spores 10 to 11 $\mu$  long, and from *M. pachyasca* Rost., with spores 16 to 20 x 5 to

<sup>73</sup> Det. Standley.

6 $\mu$ . The spores are also larger than those of *M. pullemansii* P. Henn. and *M. gaveensis* P. Henn., both from Brazil. The spores of *M. calumbi* Rehm are much smaller.

PHYSALOSPORACEAE

PHYSALOSPORA Niessl

Notiz ueber Kr. Pyr., in Verhandl. d. naturf. Vereins in Brünn, 14:10, 1876.

82. PHYSALOSPORA AGAVES P. Henn.

Engl. Bot. Jahrb., 51, 1903.

On *Fourcroya* sps.

Costa Rica: Asseri, June 26, 1923, 128.

This specimen agrees essentially with the description of the above named species, described from Africa, and differs somewhat from *P. fourcroyae* P. Henn.

83. PHYSALOSPORA CESTRI Stevens n. sp.

[Figure 75]

Spot none. Perithecia punctiform, black, subepidermal, grouped in clusters about 1 to 2 mm. in diameter, but the perithecia usually separate, sometimes two or three contiguous. Perithecia 77 to 154 $\mu$  in diameter, globose, ostiole circular, 7 to 15 $\mu$  in diameter, wall at base and sides dark, parenchymoid, 14 to 18 $\mu$  thick. Clypeus subepidermal, 15 to 20 $\mu$  thick, not equalling the diameter of the perithecium. Asci basal, 8-spored, ovate, 60 x 22 $\mu$ , short stipitate, thin-walled. Paraphyses numerous, matted. Spores oblong, hyaline, continuous, 22 x 5 $\mu$ , obtuse.

On *Cestrum* sp.

Costa Rica: Port Limon, Aug. 10, 1923, 865.

The absence of mycelium from the epidermal cells, though a clypeus is developed in the cells immediately below, is somewhat unique. The very narrow clypeus is also distinctive. Occasionally there is a slight development of stroma at the side of the clypeus, on the perithecium.

DIDYMELLA Sacc.

Mich., 1, 377.

84. DIDYMELLA EUPATORII Stevens n. sp.

[Figures 76, 77]

Spot indefinite, consisting, where stromata are numerous, of a blanched or yellowed area in the leaf. Isolated stromata are without spot. Stromata amphigenous, often on the minor veins, black, small. In section the black stroma is seen to be mainly above the locule and epidermal, as a clypeus, 36 to 50 $\mu$  thick, though hyaline stroma is found in the mesophyll to considerable distance, which in age also become black. Locules globose,

100 to 150 to 180 $\mu$  in diameter, opening epiphylloous. Ostiole sometimes through a beak, 77 x 30 $\mu$ . Asci, 8-spored, clavate, 60 x 7 $\mu$ . Paraphyses filiform, numerous. Spores hyaline, fusiform, 1-septate, 21 x 3.5 $\mu$ , several guttulate. Conidial locules subglobose, 80 x 60 $\mu$ ; conidia hyaline, continuous, oblong, 7 x 3 $\mu$ , obtuse.

On *Eupatorium* sp.

Costa Rica: La Palma, July 8, 1923, 307.

#### GNOMONIACEAE

#### GLOMERELLA Sch. and Spaulding

Sci., n. s. 17:750, 1903.

#### 85. GLOMERELLA BROMELIAE Stevens and Weedon n. sp.

Spots irregular in size and shape, from a few millimeters to several centimeters in diameter. Perithecia spherical, immersed, becoming erumpent, black, 105 to 299 $\mu$  in diameter and 105 to 237 $\mu$  deep. Asci basal, 8-spored, 74 to 81 x 17 $\mu$ , clavate, thick walled. Spores 14 to 21 x 5 to 7 $\mu$ , hyaline, nonseptate, oblong, slightly thicker at the center. Paraphyses filiform, guttulate. Pycnidial stromata, 141 to 624 x 141 to 265 $\mu$ . Pycnidial cavities 21 to 52 x 21 to 91 $\mu$ . Conidia hyaline, continuous, 10 to 21 x 4 to 5 $\mu$ .

On *Bromelia penguin*.

Costa Rica: Escasu, July 29, 1923, 166.

The perithecia are almost spherical but the ascigerous cavity is flask shaped, and varies from 95 to 123 $\mu$  in width x 123 to 130 $\mu$  in length, including the neck of the flask which is from 35 to 52 $\mu$  long x 24 to 42 $\mu$  wide. The ascigerous cavity is surrounded by a large-celled, black stroma, 70 to 88 x 133 to 176 $\mu$  deep, below the fertile portions, and 17 to 24 $\mu$  thick at the sides. Occasionally two perithecia are borne by the same stroma, separated by a heavy black wall and with the necks extending above the stroma surface. The stroma grows upward pushing into the epidermal cells and rupturing the cuticle. The conidia are in pycnidia which are scattered among the perithecia and are of similar structure, but are larger than the perithecia and appear to the naked eye to be more superficial, a little more elevated, black and hard. Microscopical examination shows them to be embedded in a stroma, erumpent and similar to that of the perithecia. Those having but a single pycnidium measure 141 to 176 $\mu$ . The conidia are slightly larger at one end than at the other; both ends are obtuse.

#### MAZZANTIA Mont.

Syll. plant. crypt., 245, 1856.

86. *MAZZANTIA ARUNDINELLAE* Stevens n. sp.

[Figures 78-80, 120]

Stroma dull black, oval or irregularly oval, 2 to 5 x 0.5 to 1.5 mm. across, immersed, subepidermal, becoming erumpent by a protruding beak or by cracking the covering epidermis. Mesostroma hyaline, of very thick walled cells, bounded by a black, compact rind about  $15\mu$  thick. Perithecia 170 to  $350\mu$  wide, deeply buried (60 to  $80\mu$ ), 80 to  $150\mu$  deep, thin walled (7 to  $8\mu$ ), wall and nearby mesostroma slightly brown. Ostiole long, up to  $150\mu$  and usually rising obliquely through the stroma, lined around its mouth by periphyses, and often projecting above the surface as a short beak. Asci 4 to 8 spored, 52 to 67 x 5 to  $7\mu$ , uniseriate. Paraphyses filiform, 42 to  $52\mu$  long. Spores 13 to 15 x 5 to  $7\mu$ , hyaline, non-septate, oval, the greatest diameter in the center, the ends rounded, one to several guttulae, heavy walled.

On *Arundinella hispida*.

Costa Rica: Peralta, July 12, 1923, 343.

The most distinctive characters of this fungus are the hyaline mesostroma, the black, thin rind, and the deeply buried ostiolate perithecia. The host cells, even when completely filled with mycelium, at first show no change in character, later however the host cell walls, throughout a considerable region, may disappear entirely, apparently being dissolved away. In some instances there is a considerable development of the hyaline stroma accompanying the dissolution of the host cells, this resulting in an increase in mass and an arching upward of the epidermis or other overlying tissues. The mycelium penetrates all of the host elements in the occupied region, even into the sclerenchyma fibers. Superficially the fungus resembles the Phyllachoraceae but the hyaline mesostroma, together with the well developed ostiole, deny relationship here. In many characters it is near *Glomerella* but its stroma is very different. Its real connection seems to be most closely with the Valsaceae or the Melanconidiaceae, though Sydow suggests the *Hyponectrieae*.<sup>74</sup>

## CLYPEOSPHAERIACEAE

## PHAEOPELTOSPHAERIA Berl.

Micr. Tosc. in N. Giorn. Bot. ital., 24:139, 1892.

87. *PHAEOPELTOSPHAERIA PANAMENSIS* Stevens and King n. sp.

[Figures 81-83]

Spot small, subcircular to oval or slightly irregular, average 0.3 x 0.6 mm. (max. observed 0.7 x 0.36 mm.), occurring singly or grouped, sometimes in a more or less linear series parallel with the veins, hypophyllous, black and glabrous, usually bordered by a narrow, light colored area.

<sup>74</sup> Ann. Mycol., 13:191, 1915.



Stromata clypeate, black, arched and continuous with the tangled mycelium at the base of the perithecium. Perithecia situated in the mesophyll near the upper leaf surface, single or sparingly cespitose, in cross section narrowly to broadly bulbiform, up to  $125\mu$  across and  $80\mu$  deep, with ostiole averaging  $33\mu$  across. Asci club-shaped, distal ends rounded, 8-spored, numerous, average  $66 \times 10\mu$ . Paraphyses numerous, filiform, up to  $82\mu$  long. Spores muriform, fusiform; olivaceous or straw colored;  $16 \times 5\mu$ . Hyphal development sparse to moderate, intercellular except for haustoria-like structures invading all of palisade and mesophyll of host leaves.

On *Chaetochloa vulpiseta* (Lam) H. and C.

Panama, Gamboa, Aug. 16, 1923, 1350.

In general appearance the spots of this fungus resemble those of *Phyllachora chaetochloae* Stevens, with which they occurred on the host. It differs from *Phaeopeltosphaeria caudata* Berl. in the form and size of the perithecia, the size of the asci, and the size and structure of the spores.

## BASIDIOMYCETES

### EXOBASIDIALES

#### MICROSTROMA Niessl

Mähren Crypt. Fl., 165, 1865.

#### 88. MICROSTROMA PITHECOLOBII Lamkey

Mycol., 12:52, 1920.

On *Pithecolobium saman*.

Costa Rica: El Roble, July 25, 1923, 137.

### AGARICALES

#### POLYPORACEAE

#### POLYPORUS Mich.

Nov. Pl. gen., 129, 1729.

#### 89. POLYPORUS FRUTICUM B. and C.<sup>75</sup>

Jour. Linn. Soc., 10:310, 1869.

On Living leaves.

Costa Rica: San Cecelia, Aug. 7, 1923, 763.

## FUNGI IMPERFECTI

### SPHAEROPSIDALES

#### HYALOSPORAE

#### PHYLLOSTICTA Pers.

Fr. Syst. Myc., 2:257.

<sup>75</sup> Det. E. A. Burt.



90. *PHYLLOSTICTA BEGONIICOLA* Stevens & Baechler n. sp.

Spots dark brown with lighter yellow margins, 2 to 5 cm. in diameter, visible on both surfaces of the leaf, irregular, indefinite. Mycelium light brown, diameter  $3\mu$ . Pycnidia immersed, dark brown to black, ostiolate, 125 to  $140\mu$ . Spores irregularly oblong, obtuse, hyaline, continuous, 7 to  $8 \times 3\mu$ .

On Begonia.

Costa Rica: Peralta, July 13, 1923, 429.

This differs from *Phyllosticta begoniae* P. Brun. in not forming a pale center in the spot and in having longer spores.

91. *PHYLLOSTICTA CHELONANTHI* Stevens n. sp.

Spots 1 to 10 mm. in diameter, subcircular, translucent, border definite, surrounded by a discolored zone 3 to 5 mm. wide that merges indefinitely with normal leaf. Young spots occupied by a single central pycnidium; older spots bearing numerous scattered pycnidia. Pycnidia  $70\mu$  in diameter, dark. Ostiole very large, nearly as large as the pycnidium. Conidia irregularly oblong, continuous, hyaline, 5 to  $7 \times 2\mu$ , obtuse.

On *Chelonanthus acutangulus*.

Costa Rica: La Palma, July 8, 1923, 284.

92. *PHYLLOSTICTA COFFEICOLA* Speg.

Revista de la Facultad de Agronomia Y. Veterinaria, La Plata, 1-2, 1895-96.

On cultivated coffee.

Costa Rica: Cartago, July 7, 1923, 261.

[Figures 84, 85, 122]

The specimens reported provisionally under this name show diseased or dead spots on the leaves, ranging from one to several centimeters in diameter. They are tan colored when young but black when old. Pycnidia are very numerous throughout the spot and visible under a hand lens. Also on the upper surfaces of the diseased areas appear fan-shaped radiations (Fig. 122). Careful study of these radiations fails to show them to be mycelial but they seem rather to be due to hypertrophy or mild intumescence of the epidermal cells, probably induced by mycelium. The following description of the fungus may be given:

Pycnidia epiphyllous, rarely hypophyllous, developing at first subcuticular but later pressing down through the palisade tissue, circular,  $110\mu$  in diameter, straw colored, ostiole irregular, with slightly dark border. Spores hyaline, continuous, oblong, 5 to  $7 \times 2\mu$ , obtuse.

The pycnidial wall is very tenuous and is, together with the overlying cuticle, easily knocked off leaving the spore bed uncovered and thus suggesting that the fungus is not of the Sphaerioidaceae, though earlier stages clearly show that it is so.

Agreement with Spegazzini's description is not very close nor does he mention the peculiar surface radiation. It is therefore quite possible that this is a distinct species.

The original description of this species is as follows: "Maculae orbiculares majusculae arescenti-albidae; perithecia epiphylla parenchymate immersa lenticularia (180–200 $\mu$ ) atra glabra, ostiolata, contextu parum distincto; sporulae cylindraceae utrinque obtusiusculae atque minute 1-guttulatae, continuae hyalinae.

Hab. Ad. folia viva et languida Coffeae arabicae."

MACROPHOMA (Sacc.) Berl. and Vogl.

Atti. Soc. Veneto-Trentina, 172, 1886.

93. MACROPHOMA PANDANI (Lev.) Berl. and Vogl.

Atti. Soc. Veneto-Trentina, 172, 1886.

*Phoma pandani* (Lev.) Sacc. Syll. Fung., 3:157, 1884.

*Sphaeropsis pandani* Lev. (not *S. pandani* P. Henn.) Am. Sc. Nat., 293, 1846.

On *Pandanus* sp.

Costa Rica: Peralta, July 11, 1923, 337.

The descriptions of *M. pandani* are very meager, no spore measurements being given, but in so far as the description goes it is in agreement with our specimen, the following description of which we give:

Forming dark spots on the bases of *Pandanus* fruits. Mycelium pale yellow, 3 $\mu$  in diameter. Pycnidia 190 $\mu$  in diameter, immersed, brown, ostiolate. Spores vary in size, largest 25 x 14 $\mu$ , hyaline, granular, thin walled, continuous.

#### PHAEODIDYMAE

Botryodiplodia Sacc.

94. Botryodiplodia sp.

[Figure 86]

The specimens which are immature may be described as follows:

Spot brown, involving large area of the leaf. Pycnidia 155 to 180 $\mu$ , numerous, black, immersed, ostiolate, erumpent. Spores 22 to 25 x 3 to 14 $\mu$ , one-celled, hyaline. Paraphyses 38 to 55 $\mu$  in length.

On *Dracaena* sp.

Costa Rica: Guapiles, July 18, 1923, 508.

On crushing open a pycnidium spores of all sizes up to the maximum are found and their connection with their conidiophores is clearly evident. Between the conidiophores arise long slender, comparatively straight, paraphyses.

## HYALODIDYMAE

## DARLUCA Cast.

Cat. Pl. Marseill. Suppl., 53.

## 95. DARLUCA FILUM (Biv.) Cast.

Cat. Pl. Marseill. Suppl., 53.

On Puccinia.

On *Zea Mays*.

Costa Rica: Experiencia Farm, July 17, 1923, 520.

## SCOLECOSPORA

## SEPTORIA Fr.

Syst. Myc. 3:480.

## 96. SEPTORIA CAVENDISHIAE Stevens n. sp.

[Figure 87]

Spots subcircular to irregular, definite, 3 to 15 mm. in diameter, extending through the leaf, centers tan-colored, borders red, 0.5 mm. wide, slightly raised. Pycnidia black, punctiform, opening epiphyllous, about  $100\mu$  in diameter, erumpent, ostiolate, base in the palisade tissue, about  $230\mu$  long. Spores filiform, slightly thicker in the middle and tapering toward the ends, hyaline, 3-septate,  $25$  to  $32 \times 3.5\mu$ .

On *Cavendishia* sp.

Costa Rica: Cartago, June 23, 1923, 51.

## 97. SEPTORIA ERIGERONTIS B. and C.

North Amer. Fungi. n. 437, in Ann. and Mag. Nat. Hist.

On *Erigeron* sp.

Costa Rica: La Palma, July 8, 280.

## 98. SEPTORIA LOBELIAE Peck.

Report of the Botanist, N. Y. State Mus. Nat. Hist., 187, 1870.

On *Lobelia laxiflora*.

Costa Rica: Agua Caliente, July 5, 1923, 220.

## MELANCONIALES

## COLLETOTRICHUM CORDA

Sturm Cr. Fl., III, 3:41.

## 99. COLLETOTRICHUM IRESINES Stevens n. sp.

Spots irregularly circular, definitely bordered, ashen gray, 5 to 8 mm. in diameter, extending through the leaf. Acervuli  $80$  to  $90\mu$  in diameter, densely setose. Setae wine colored to black, crooked, irregular, obtuse,

septate, about  $60\mu$  long,  $3.5\mu$  thick. Conidia oblong, straight, obtuse, hyaline, 12 to  $18 \times 4\mu$ .

On *Iresine calcaea*.<sup>76</sup>

Costa Rica: Desamparados, June 24, 1923, 139.

100. COLLETOTRICHUM PEREGRINUM Passer.

Diagn. F. N. IV, 14.

On *Polyscias quilfoylei*.

Panama: Panama, Aug. 13, 1923, 1002.

Large blanched spots on the leaves were so numerous as to seriously disfigure the foliage and injure the vigor of the plants. The disease was quite common in the Canal Zone.

MONILIALES

MONILIACEAE

OIDIUM (Link) em. Sacc.

Mich., 2:15, 1880.

101. OIDIUM

Probably of *Sphaerotheca humuli* var. *fuliginea* (Schlecht) Salm. Berl. Ges. Nat. Freund. Verh., 1:47, 1819.

On *Erigeron* sp.

Costa Rica: San José, June 20, 1923, 4; Desamparados, June 27, 1923, 135.

102. OIDIUM.

Probably of *Sphaerotheca humuli* (DC.) Burr. Bull. Ill. State Lab. Nat. Hist., 2:400, 1887, or of *S. pannosa* Lev. Ann. Sci. Nat., III, 15:138, 1851.

On *Rosa* sp. (cultivated).

Costa Rica: Alajuela, July 29, 1923, 654.

103. OIDIUM sp.

On *Erythrina* sp.

Costa Rica: Aserri, June 26, 1923, 125.

On *Tabebuia* sp.

Costa Rica: San Vicente del Coronado, June 30, 1923, 177.

104. OIDIUM.

Probably of *Microsphaera diffusa* Cooke and Peck, Journ. Bot., II, 1:13, 1872.

On *Meibomia* sp.

Costa Rica: Desamparados, June 27, 1923, 146.

<sup>76</sup> Det. Standley.

## BOTRYTIS Mich.

Nov. gen., 212, 1729.

## 105. BOTRYTIS CINEREA (group) Pers.

Syn., 690, 1801-1808.

On *Rosa* sp. (cult.).

Costa Rica: Cartago, July 6, 1923, 227.

## RAMULARIA Ung.

Exanthem. 169.

## 106. RAMULARIA TARAXICI Karst.

Fragmenta. Mycol., 6:7.

On *Taraxacum* sp.

Costa Rica: San José, July 28, 1923, 648.

In the description of *Ramularia* as given in Saccardo's *Sylloge Fungorum* the spores are typically 2-septate, though species are given in the same volume as having 1-septate spores. The present species in a count of 42 spores gives 4-continuous, 36 1-septate, one 3-septate. Notwithstanding this apparent disagreement with the generic description we find by comparison with specimens in various exsiccatti that the spores in these specimens show similar septation.

## DEMATIACEAE

## CLADOSPORIUM Link

Mag. Ges. Naturf. Freude Berlin, 8:37, 1816. Sp. pl. Fungi, 1:39, 1824, Sacc. Mich., II, 27.

## 107. CLADOSPORIUM FULVUM Cooke.

Rav. Amer. Fungi, n. 5599; Grev. 1883, p. 32.

On *Solanum lycopersicum* (Tomato).

Costa Rica: El Roble July 25, 1923, 639.

## HELMINTHOSPORIUM Link

Berl. Mag., 3:10, 1809, em Sacc. Mich., 2:28.

## 108. HELMINTHOSPORIUM MAYAGUENZENSE Miles.

Trans. Ill. Acad. Sc., 10:253, 1917.

On *Paspalum conjugatum*.<sup>77</sup>

Costa Rica: Peralta, July 13, 435; July 11, 335; July 13, 456; Sebario, Aug. 8, 815.

Panama: Juan Mina, Aug. 18, 1167.

On *Isachne arundinacea*.<sup>77</sup>

Costa Rica: Siquirres, July 31, 1923, 678.

<sup>77</sup> Det. Chase.



109. *HELMINTHOSPORIUM RAVENELII* Curtis and Berk.

North Amer. Fungi, n. 628 and Cub. Fung. n. 627.

On *Sporobolus* sp.

Panama: Frijoles, Aug. 20, 1923, 1192.

Costa Rica: San José, June 20, 1923, 13; Desamparados, June 27, 1923, 133; Cartago, July 2, 1923, 188.

On *Sporobolus berteroaensis*.<sup>77</sup>

Costa Rica: Cartago, July 7, 1923, 269; Peralta, July 12, 1923, 361

## CERCOSPORA Fres.

Beitr. Zur. Mykol., 90, 1850.

110. *CERCOSPORA ALABAMENSIS* Atk.

Jour. Elisha Mitchell Sc. Soc., 8: part 2, 51, 1891.

On *Ipomoea pes-caprae*.

Costa Rica: Puntarenas, July 24, 1923, 617.

111. *CERCOSPORA COFFEICOLA* B. and C.

Grevillea 9:99, 1881.

On *Coffea arabica*.

Costa Rica: Cartago, July 7, 1923, 262.

112. *CERCOSPORA COSTI* Stevens, n. sp.

Spot irregular, blanced, or ashen due to conidiophores, definitely bordered, sometimes involving a whole leaf. Conidiophore clumps exstomatal, up to  $36\mu$  in diameter, containing very numerous conidiophores. Conidiophores simple, straw colored to yellow, very short (usually  $14\mu$  or less),  $3\mu$  thick, straight, rigid. Conidia slender, whip-shaped, tapering slightly, hyaline, moderately curved, up to  $82\mu$  long,  $3\mu$  thick, several-septate, mycelium straw colored.

On *Costus* sp.

Panama: Gatun, Aug. 24, 1923, 1343.

113. *CERCOSPORA DIFFUSA* E. and E.

Journ. Myc., 3, 1888.

On *Solanum nigrum*.

Costa Rica: San José, June 20, 1923, 6.

Peralta, July 13, 1923, 450.

114. *CERCOSPORA ERECHTITES* Atk.

Jour. Elisha Mitchell Sc. Soc. (Chapel Hill, N. C.), 8:pt. 2:33, 1892.

On *Erechtites* sp.

Costa Rica: Experiencia Farm, July 18, 1923, 556.

This specimen agrees with the original description by Atkinson, except that he gives the spore dimensions as 70 to 230 x 3 to 4 $\mu$ , whereas in this material the spores measure 37 to 80 x 3 to 5 $\mu$ .

115. *CERCOSPORA NICOTIANAE* E. and E.

Proc. Acad. Nat. Sci. of Phil., p. 170, 1893.

While working on a leaf spot of tobacco supposedly caused by *Cercospora nicotianae*, it was found that the fungus did not agree in all respects with the original description of *Cercospora nicotianae* by Ellis and Everhart. The main point of variance was in the length of the hyphae which, in the original description, is given as 75-100  $\mu$  x 5 $\mu$ , while the hyphae of the fungus examined, averaged 188 x 4 $\mu$ . Specimens from the University Herbarium and the State Natural History Survey proved to be of the short hyphae type and therefore agreed with the original description of *Cercospora nicotianae*.

The length of the hyphae was not considered as a variation within the species since no variation was found within a particular disease spot and since the hyphae are in many cases twice as long as the short stubby type. The *Cercospora* is therefore regarded as being a new species but the lack of sufficient material at present prevents it being described as such.

116. *CERCOSPORA POROPHYLLI* Stevens and Moore n. sp.

Amphigenous, fruiting mostly on lower surface. Spots circular, center cinereous, 3 to 8 mm. in diameter, surrounded by a black ring 1 to 2 mm. wide; the entire area between spots becoming brown or smoky brown; spot on both leaf surfaces. Conidiophores brown, erect in clusters from the stomata, 40 to 80 $\mu$  long, 5 to 8 $\mu$  wide at the base, tapering slightly, geniculate in the upper half. Conidia hyaline, 40 to 60 $\mu$  long, 3 to 4 $\mu$  wide, straight, cylindrical or tapering toward apex, 1 to 5 septate, not constricted.

On *Porophyllum ruderale*.<sup>78</sup>

Costa Rica: Siquirres, July 18, 1923, 554.

No *Cercospora* is reported on *Porophyllum* nor any closely related genus. *C. jacquiniana* Thüm, more nearly resembles this species than any other, but is easily distinguished by the yellow spots and arcuate conidia.

117. *CERCOSPORA PURPUREA* Cke.

Grev., 7:34, 1878.

On *Persea gratissima*.

Panama: Frijoles, Aug. 20, 1923, 1191.

These specimens agree reasonably well with the rather meager description given in the *Sylloge Fungorum*, except that in my specimens the conidiophores are always short, seldom exceeding 56 $\mu$ , while the description reads 50 to 70 $\mu$ .

<sup>78</sup> Det. Standley.

118. *CERCOSPORA SAMBUCI* Stevens and King. n. sp.

Spots round, suboval, sometimes irregular, solitary or confluent, extending through leaf, silvery or ashen gray in centers with distinct, somewhat raised, crenulate, brownish border with surrounding purplish coloration, 1 to 5 mm. in diameter; conidiophores amphigenous, much more prominent on the upper surface, in dense tufts, brownish, becoming sparingly septate with age, straight or bent, 30 to 80 x 3 to 5 $\mu$ . Conidia cylindrical, borne acrogenously, straight or curved, apical end narrowly rounded, base slightly narrowed, hyaline, 1 to 5 usually 3 or 4 septate, 24 to 69 x 3 to 5 $\mu$ .

On *Sambucus mexicana*.<sup>79</sup>

Costa Rica: Cartago, July 7, 1923, 250.

There have previously been two species and a subspecies of *Cercospora* reported upon *Sambucus*, viz.: *C. catenospora* Atk., *C. depazeoides* (Desm.) Sacc., and *C. depazeoides* subsp. *sambucina* Ell. and Kell. The purplish coloration surrounding the spots on affected leaves does not occur in *C. catenospora*, neither are the conidiophores similar to those of this fungus. The spores of *C. depazeoides*, and also its subspecies *sambucina* differ from our fungus in form and septation as well as coloration.

## STILBACEAE

## ISARIA Pers.

Tent. Disp. meth. fung., 41, 1797.

119. *ISARIA PALMAE* Stevens and King n. sp.

Coremia generally erect, numerous, distributed over the substratum, each composed of closely united, parallel hyphae, all of which terminate singly on the periphery or apex. Coremia cylindrical or somewhat arcuate, sometimes tapering apically, length up to about 1 mm., width 40 to 100 $\mu$  or more, white. Hyphae composing coremium non-septate, simple, hyaline, 1.75 to 2 $\mu$  thick, length up to 1 mm., apex slightly dilated and sporiferous, a short irregular ring forming and extending the apex each time a spore is formed. Spores borne singly on hyphae on sides and apex of coremium, suboval, hyaline, 3 to 3.8 x 3.8 to 5 $\mu$ .

On the inflorescence of palm.

Panama: Frijoles, August 20, 1923, 1206.

## STILBELLA Lindau

Engler-Prantl, Nat Pflanzenfamilien, 1-1<sup>xx</sup>, 489, 1900.

120. *STILBELLA PROLIFERANS* Stevens n. sp.

[Figure 88]

Coremia in groups on the surface of bark, 600 to 700 $\mu$  tall, 30 to 125 $\mu$  thick, simple or branched; stalk-colorless, smooth, straight, composed of

<sup>79</sup> Det. Blake.

parallel hyphae about  $1\mu$  thick. Heads red, 60 to  $310\mu$  in diameter, flat-topped. Conidiophores simple. Conidia acrogenous, not catenulate but accumulating in large numbers on the top of the head, oval, hyaline, 1-celled, 5 to  $6 \times 3\mu$ , obtuse.

On *Theobroma cacao*.

Costa Rica: Indiana branch, July 18, 1923, 541.

The distinctive character of this species is the branching of the coremia by proliferation. A coremium may produce its head and quantities of spores, then growth may be resumed at one or more places on the surface of the head and a new coremium superimposed on the old. This may result in quite complicated branching systems. Fig. 88. In other instances there may be only one proliferation on a head, then only one on the secondary head etc., for several repetitions.

#### TUBERCULARIACEAE

##### FUSARIUM Link.

Berl. Mag., 3:10, 1809.

#### 121. FUSARIUM GRAMINUM Cda.<sup>80</sup>

On *Paspalum virgatum*.<sup>81</sup>

Panama: Frijoles, Aug. 20, 1923, 1194.

Very numerous spikelets were overgrown with an orange colored, somewhat viscous, coating so conspicuous as to be visible at considerable distance.

##### PUCCINIOPSIS Speg.

F. Guar., 2:n. 202, 1888.

#### 122. PUCCINIOPSIS CARICAE Earle.

Bull. N. Y. Bot. Gard., 2:340, 1902.

On *Carica papaya*.

Costa Rica: San Cecelia, Aug. 7, 1923, 757.

Panama: Gamboa, Aug. 16, 1923, 1084.

The Pucciniopsis is attached by a fungus showing a thin hyaline mycelium and slender brown conidiophores. No conidia were seen.

##### SCENOMYCES Stevens n. gen.

[Figures 89-91, 114, 123, 124, 125]

The fungus is strictly superficial on the lower sides of leaves. The mycelium is abundant, rather generally distributed over the leaf surface as a loose net. The individual threads are about  $3\mu$  thick, yellow, translucent, straight walled, not gelatinous.

<sup>80</sup> Det. Sherbakoff.

<sup>81</sup> Det. Chase.



In numerous places over the leaf, Fig. 123, are scattered mycelial aggregations of somewhat stellate shape, Figs. 123 to 125, which suggest perithecia or pycnidia. They will hereafter be referred to as perithecia though there is no proof that they are such. These range in extreme diameter from 1 to 1.2 mm. The number of rays varies from 4 to 6, Figs. 123 to 125, most commonly 5. The center of the perithecium where the rays meet is the most elevated point, making the perithecium about 77 to 107 $\mu$  high and sloping evenly along each ray to the level of the leaf surface. From the ray laterally the mycelium is given off on both sides at acute angles, strictly parallel and contiguous, Fig. 90. Where these parallel threads meet the leaf surface the mycelium becomes irregularly arranged in a much tangled network. Fig. 89. From the apex, the ridge, of a ray more or less loose mycelium arises as a kind of a crest, and at the distal extremity of a ray, where it comes in contact with the leaf there is a pronounced bushy tuft of loose mycelium, usually some 230 $\mu$  long. Frequently the upper region of the perithecium is somewhat more densely thatched than the remaining portion. In most cases the apex of the perithecium, where the several rays meet, is occupied by a thick mat of mycelium.

In other cases the center bears a clean cut, circular hole, through which, in looking down upon it through the microscope, the bare leaf surface may be seen below. Whether this hole is normal or whether it is produced by some insect or other means is unknown.

Microtome sections of perithecia show the parallel roofing structure to be only one of two layers of mycelium in thickness. The floor is 7 to 36 $\mu$  thick and composed of a very loosely woven mycelium. The space below the cover and the leaf is occupied by a very loose network of mycelium, Fig. 91.

Most diligent search has failed to reveal any spores, conidia, or asci other than a few of varying character, probably strays. The perithecium appears to begin by the laying down of the basal outline as a region of especially dense mycelium, Fig. 89, and from these the parallel mycelium rises to meet at the ridge. The mycelium is of the general type so common in the Perisporiaceae.

In view, however, of the extremely unique characters presented, and even in the absence of spores the above description is given and the name *Scenomyces perplexans* is suggested.

On unknown dicotyledonous host.

Panama: Alehjuela, Aug. 18, 1923, 1028.



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<i>Myrcia costaricensis</i>	<i>Catacouma costaricensis</i>
<i>Myroxylon ellipticum</i>	<i>Ceratochaetopsis costaricensis</i>
<i>Nectandra glabrescens</i>	<i>Trabutia xylosmae</i>
<i>Ocotea</i> sps.	<i>Phyllachora litseae</i>
<i>Olyra latifolia</i>	<i>Phyllachora ocoteicola</i>
<i>Oplismenus burmanni</i>	<i>Dimeriella olyrae</i>
<i>Palm</i>	<i>Phyllachora oplismeni</i>
	<i>Phragmocarpella puiggarii</i>
	<i>Dothidina costaricensis</i>
	<i>Cocconia palmae</i>
	<i>Isaria palmae</i>
	<i>Schweinitziella palmigenum</i>
<i>Pandanus</i> sp.	<i>Macrophoma pandani</i>
<i>Panicum haenkeanum</i>	<i>Balansia discoidea</i>
<i>Paspalum conjugatum</i>	<i>Helminthosporium mayaguense</i>
	<i>Phyllachora paspalicola</i>
<i>fasciculatum</i>	<i>Phyllachora chaetochloae</i>
<i>virgatum</i>	<i>Fusarium graminum</i>
<i>Pennisetum distachyum</i>	<i>Phyllachora chaetochloae</i>
<i>Persea gratissima</i>	<i>Cercospora purpurea</i>
<i>Picramnia antidesma</i>	<i>Phyllachora picramniae</i>
<i>bonplandiana</i>	<i>Phyllachora picramniae</i>
<i>Piper</i>	<i>Meliola glabroides</i>
<i>Pithecolobium saman</i>	<i>Microstroma pithecolobii</i>
<i>Plantago hirtella</i>	<i>Mycosphaerella plantaginicola</i>
<i>Podachaenium eminens</i>	<i>Phyllachora ambrosiae</i>
<i>Podocarpus</i> sp.	<i>Corynelia</i> sps.
<i>Polyscias quilfoylei</i>	<i>Colletotrichum peregrinum</i>
<i>Porophyllum ruderales</i>	<i>Cercospora porophylli</i>
<i>Psychotria brachiata</i>	<i>Tonduzia psychotriae</i>
<i>Puccinia</i>	<i>Darluca filum</i>
<i>Quercus eugenifolia</i>	<i>Rheumatopeltis querci</i>
<i>Rosa</i> (cult)	<i>Oidium</i> probably of <i>Sphaerotheca humuli</i>
	var. <i>fuliginea</i>
<i>Rosa</i> sp. (cult)	<i>Botrytis cinerea</i>
<i>Rourea glabra</i>	<i>Phyllachora panamensis</i>
<i>Rubiaceae</i>	<i>Phaeodothis costaricensis</i>
<i>Sambucus mexicana</i>	<i>Cercospora sambuci</i>
<i>Schistocarpha hoffmanni</i>	<i>Phyllachora schistocarphae</i>
<i>Scleria melaleuca</i>	<i>Sphaerodothis scleriae</i>
<i>pterota</i>	<i>Sphaerodothis scleriae</i>
<i>Serjania mexicana</i>	<i>Phyllachora sapindacearum</i>
<i>Solanum lycopersicum</i>	<i>Cladosporium fulvum</i>
<i>Solanum nigrum</i>	<i>Cercospora diffusa</i>
<i>Sophoelesia</i> sp.	<i>Sphaerodothis circumspecta</i>
<i>Sporobolus berteroi</i>	<i>Helminthosporium ravenelii</i>
	<i>Dothichloe atramentosa</i>
<i>Struthanthus</i>	<i>Polystomella costaricensis</i>
<i>Stylosanthes</i> sp.	<i>Parodiella perisporioides</i>
<i>Tabebuia</i>	<i>Oidium</i> sp.
<i>Taraxacum</i>	<i>Ramularia taraxaci</i>
<i>Tetracera volubilis</i>	<i>Hyalomeliolina costaricensis</i>

Theobroma cacao  
Trophis racemosa  
Vaccinium  
Vernonia canescens  
Vigna vexillata  
Vismia guianensis  
Xylosma salzmanni  
Zanthoxylon sps.  
Zea mays  
" "

Stibella proliferans  
Phyllachora trophis  
Sphaerodothis circumscripta  
Pseudoparodiella vernoniae  
Synchytrium decipiens  
Phyllachora vismiae  
Trabutia xylosmae  
Catacouma zanthoxyli  
Phyllachora maydis  
Darluca filum



## PLATE I

## Explanation of PLATE I

Figs. 1, 2, *Synchytrium boerhaaviae*.

Fig. 1. Two resting spores within one host cell.

Fig. 2. A sporangial sorus.

Fig. 3, *Acrospermum folliicolum*.

Fig. 3. Drawing showing ascigerous portion of the perithecium, the stipe, and the ostiole.

Figs. 4, 5, *Myrianginella costaricensis*.

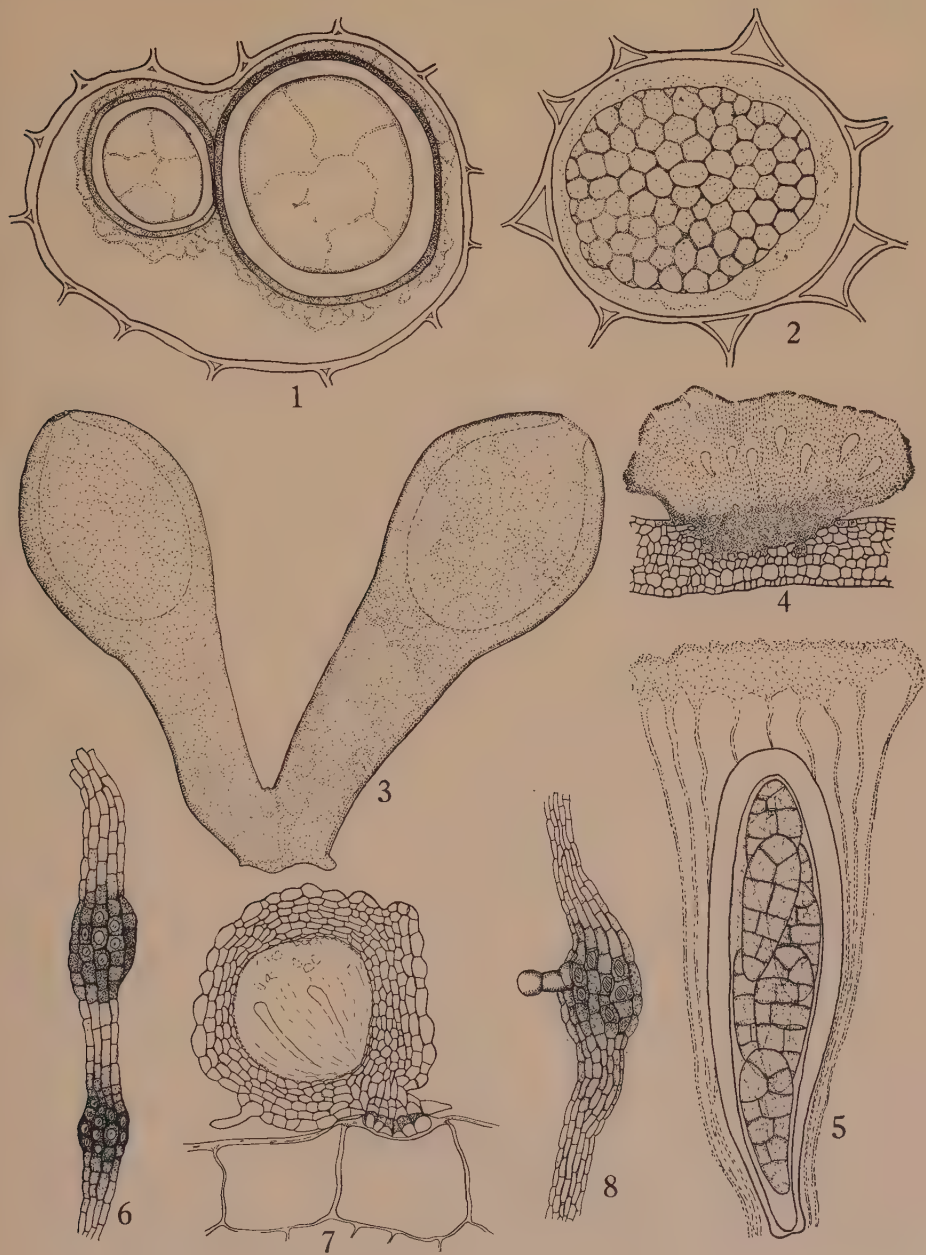
Fig. 4. Section of a stroma showing location of the asci and foot.

Fig. 5. Ascus and spores.

Figs. 6, 7, 8, *Pseudoparodiella vernoniae*.

Figs. 6, 8. Views of the subcuticular subiculum as seen from above.

Fig. 7. Perithecium in section showing the subcuticular subicle.





## PLATE II



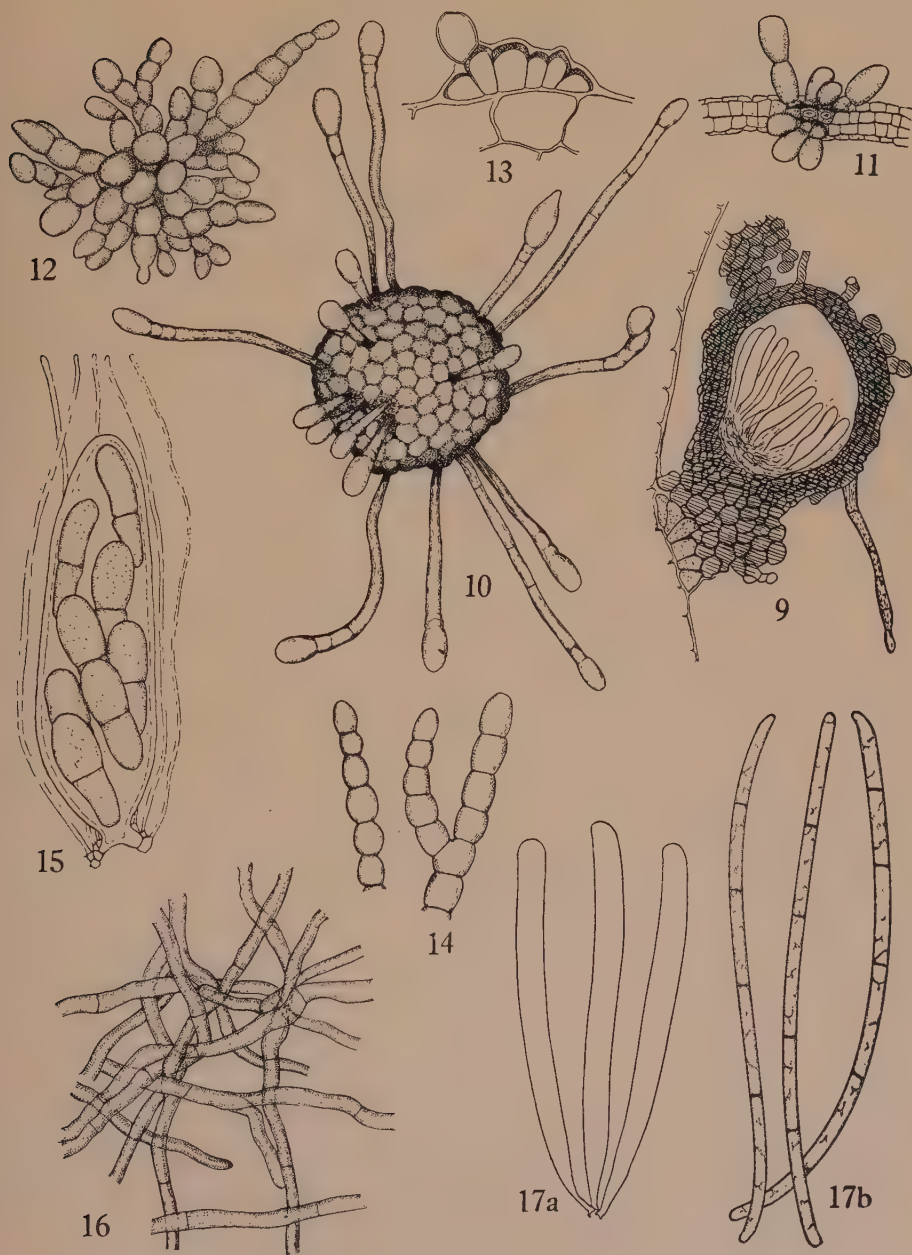
## Explanation of PLATE II

Fig. 9-15, *Pseudoparodiella vernoniae*.

- Fig. 9. Perithecium in section showing subicle.
- Fig. 10. A perithecium with setae.
- Fig. 11. Portion of a subiculum as seen from above.
- Fig. 12. A group of conidia as seen from above.
- Fig. 13. Detail of a conidiophore bed in section, showing subicle.
- Fig. 14. Conidia in chains.
- Fig. 15. An ascus and spores, paraphyses.

Figs. 16, 17a, 17b, *Tonduzia psychotriae*.

- Fig. 16. Mycelium.
- Fig. 17a. Asci.
- Fig. 17b. Spores.





## PLATE III

## Explanation of PLATE III

Fig. 18, *Chaetostigme cordiae*.

Fig. 18. An ascus, spores and paraphyses.

Fig. 19, *Dimeriellopsis costaricensis*.

Fig. 19. Conidiophores and conidia.

Fig. 20, *Dimerina dodonaeae*.

Fig. 20. Asci and spores.

Figs. 21-23, *Perisporina dentritica*.

Fig. 21. A conidiophore showing origin from the basal mycelium.

Fig. 22. A conidiophore showing intricate branching.

Fig. 23. Conidia.

Fig. 24, *Cocconia palmae*.

Fig. 24. Ascus and spores.

Figs. 25, 26, *Polystomella costaricensis*.

Fig. 25. Section of a stroma showing ascigerous locules, also conidial locules.

Fig. 26. Detail drawing showing the mycelium within the epidermal cells.



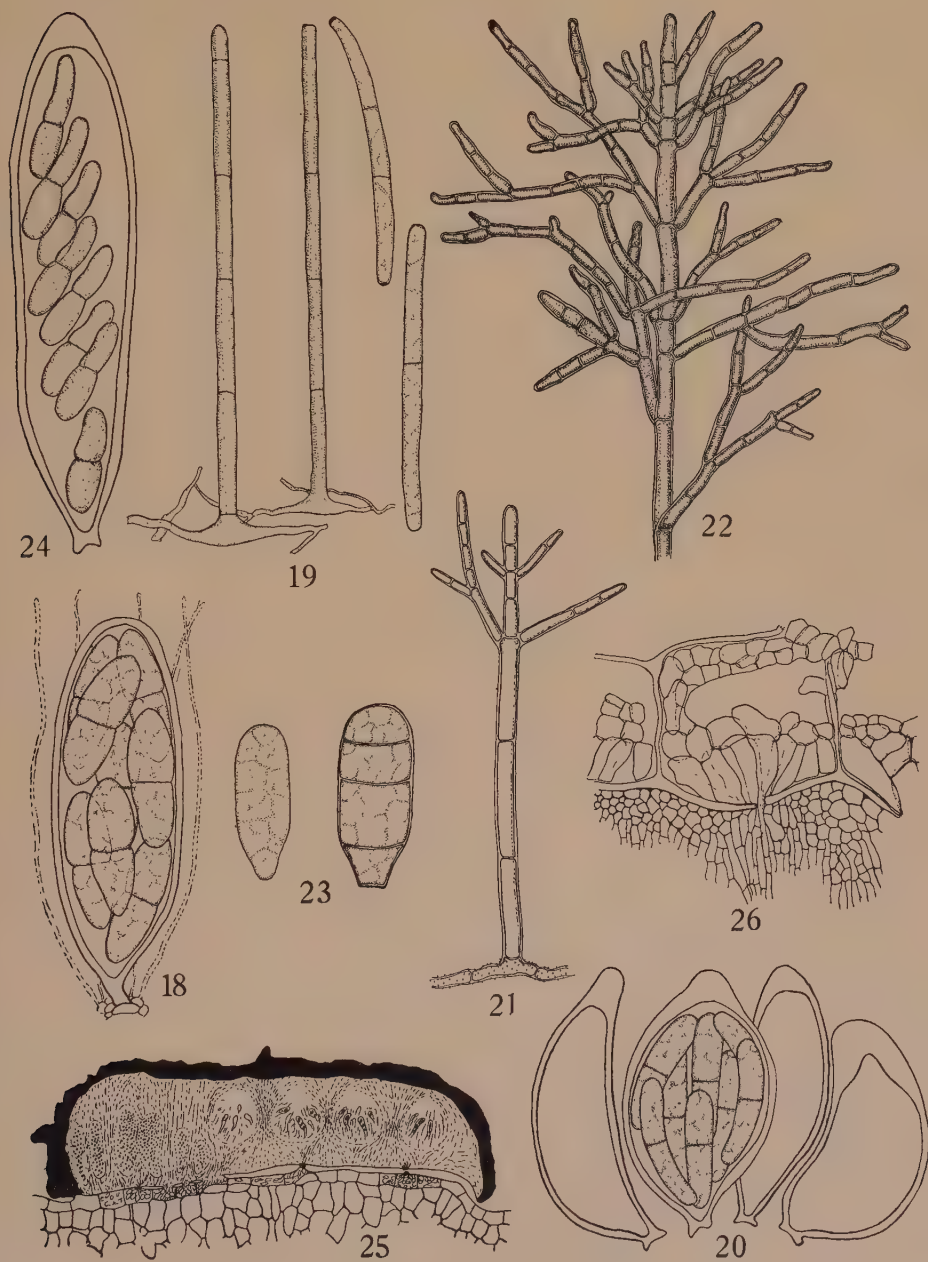




PLATE IV

## Explanation of PLATE IV

Figs. 27-31, *Rheumatopeltis querci*.

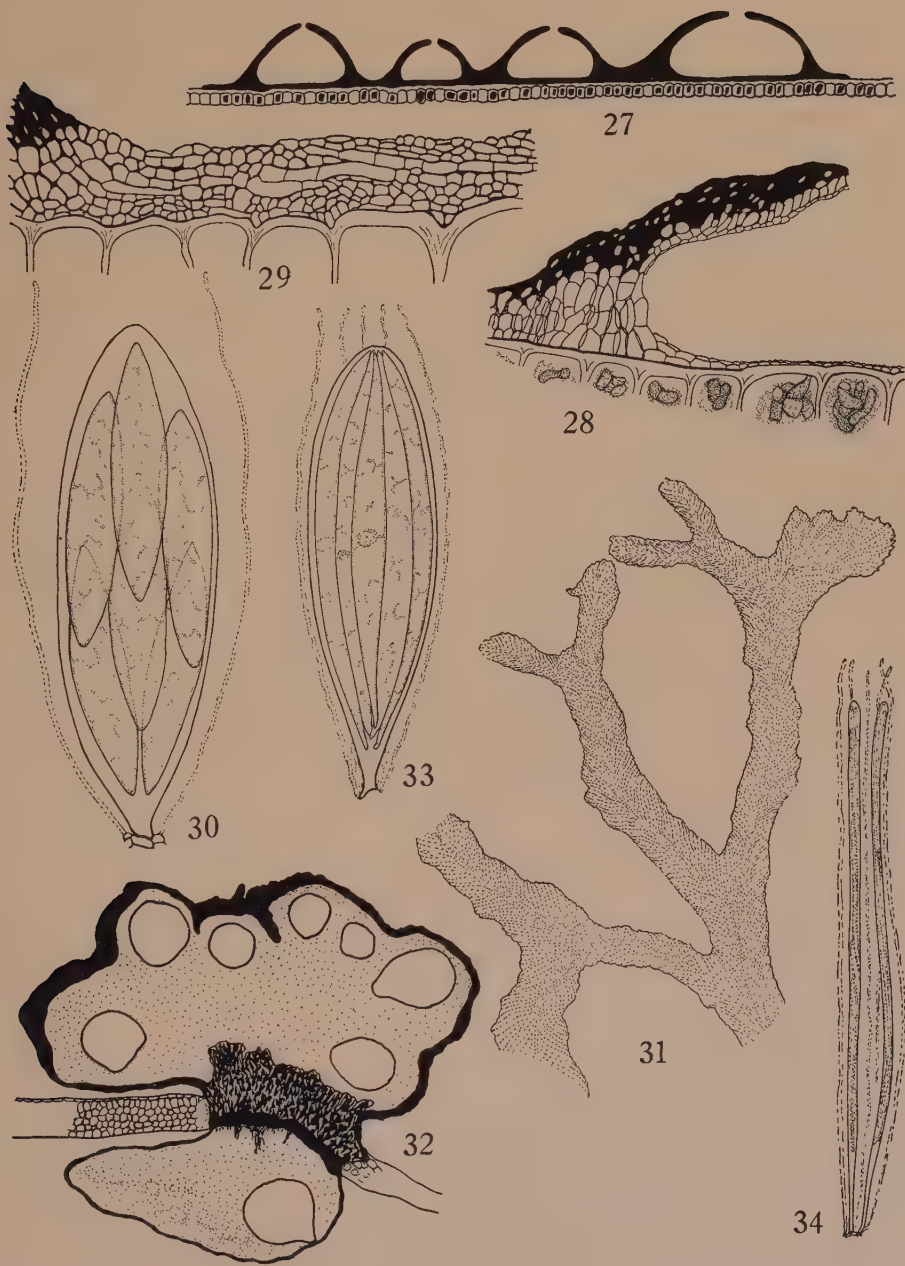
- Fig. 27. General view of stroma in section.  
Fig. 28. A portion of a stroma, showing dothideoid character, thin floor and the one locule; epidermal cells with mycelium.  
Fig. 29. A stroma showing structure of the extra-loculiferous region.  
Fig. 30. An ascus, spores and paraphyses.  
Fig. 31. Sketch showing the course of the mycelium in the thallus as viewed from above.

Figs. 32, 33, *Schweinitsziella palmigena*.

- Fig. 32. Diagram showing relation of stroma, foot, locules, hypostroma, and host tissue  
Fig. 33. An ascus, spores, and paraphyses.

Fig. 34, *Scolecoccoidea costaricensis*.

- Fig. 34. Ascus and spores.





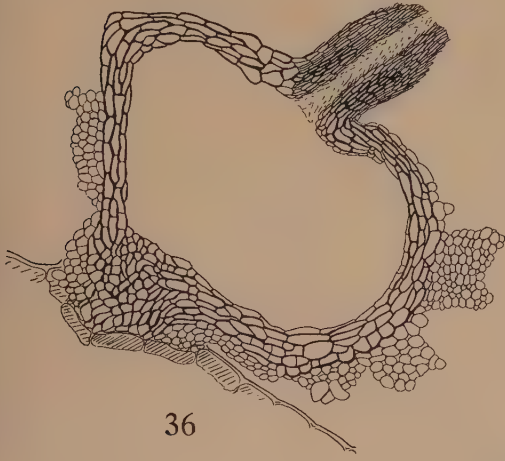


## PLATE V

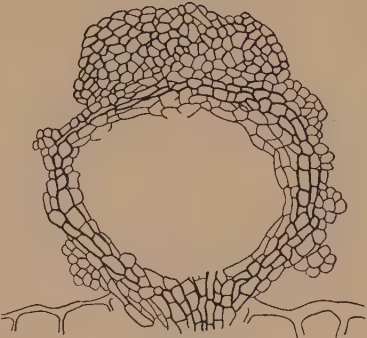
## Explanation of PLATE V

Figs. 35-40, *Hyperus costaricensis*.

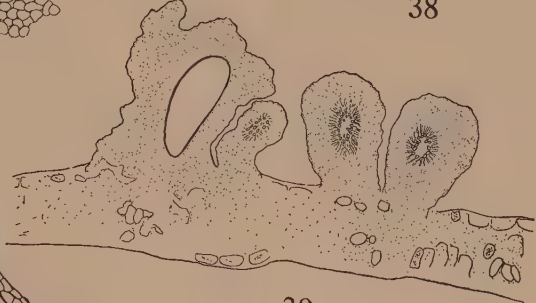
- Fig. 35. A conidial stroma, conidiophores, and conidia.
- Fig. 36. An ascigerous stroma showing the locule and rostrum.
- Fig. 37. A stroma with perithecium and remains of stroma around the perithecium.
- Fig. 38. A perithecium with remnant of stroma upon it.
- Fig. 39. A group of conidial and ascigerous stromata.
- Fig. 40. Conidiophores and conidia.



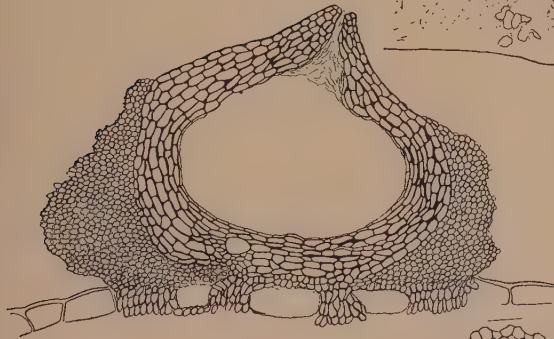
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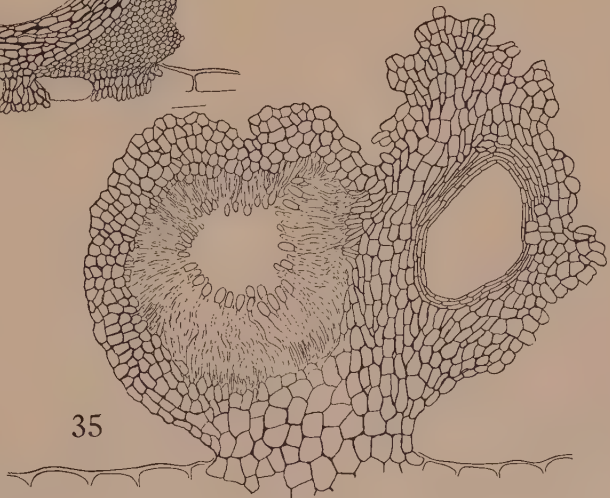
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## PLATE VI

## Explanation of PLATE VI

Figs. 41-43, *Dothidina costaricensis*.

Fig. 41. Section of a stroma showing locule and dothideoid structure.

Fig. 42. A septate ascus and spores.

Fig. 43. An ascus breaking into single-spored segments.

Figs. 44, 45, *Achorella costaricensis*.

Fig. 44. Diagram showing structure of diseased leaf, also the loculiferous stroma in the leaf with its foot.

Fig. 45. Drawing showing normal leaf structure.

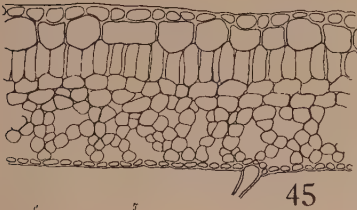
Fig. 46, *Trabutia xylosmae*.

Fig. 46. Ascus, spores, and paraphyses.

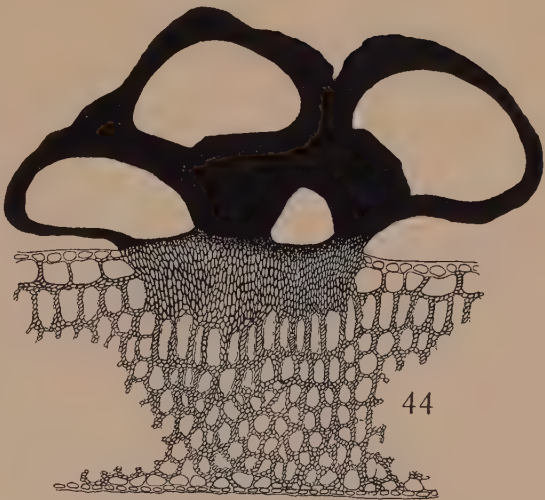
Figs. 47, 48, *Hypostigma polyadelphae*.

Fig. 47. Two stromata with connecting hyaline mycelium.

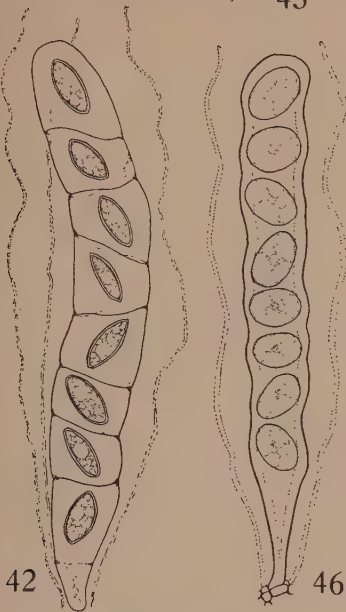
Fig. 48. A stroma in section.



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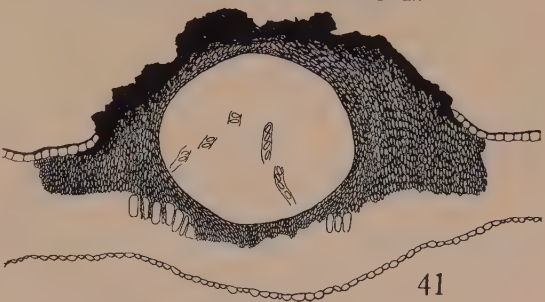


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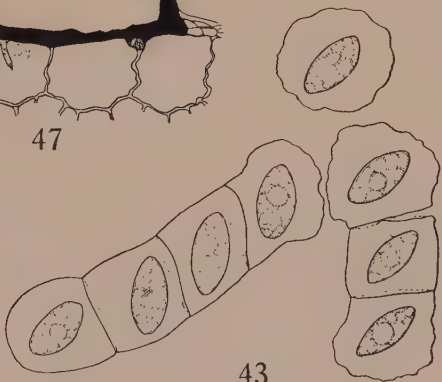
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47



48



43



## PLATE VII



## Explanation of PLATE VII

Figs. 49-52, *Hypostigma polyadelphe*.

- Fig. 49. A thallus, without perithecium, showing shape of cells at center and at margin.  
Fig. 50. A thallus bearing a perithecium showing cellular structure of the perithecial covering and projections from the base.  
Fig. 51. A thallus bearing a perithecium. The covering layer of the perithecium has been largely broken away revealing the thallus below.  
Fig. 52. Detail of the subcuticular stroma and portion of a perithecium.

Figs. 53, 54, *Catacauma zanthoxyli*.

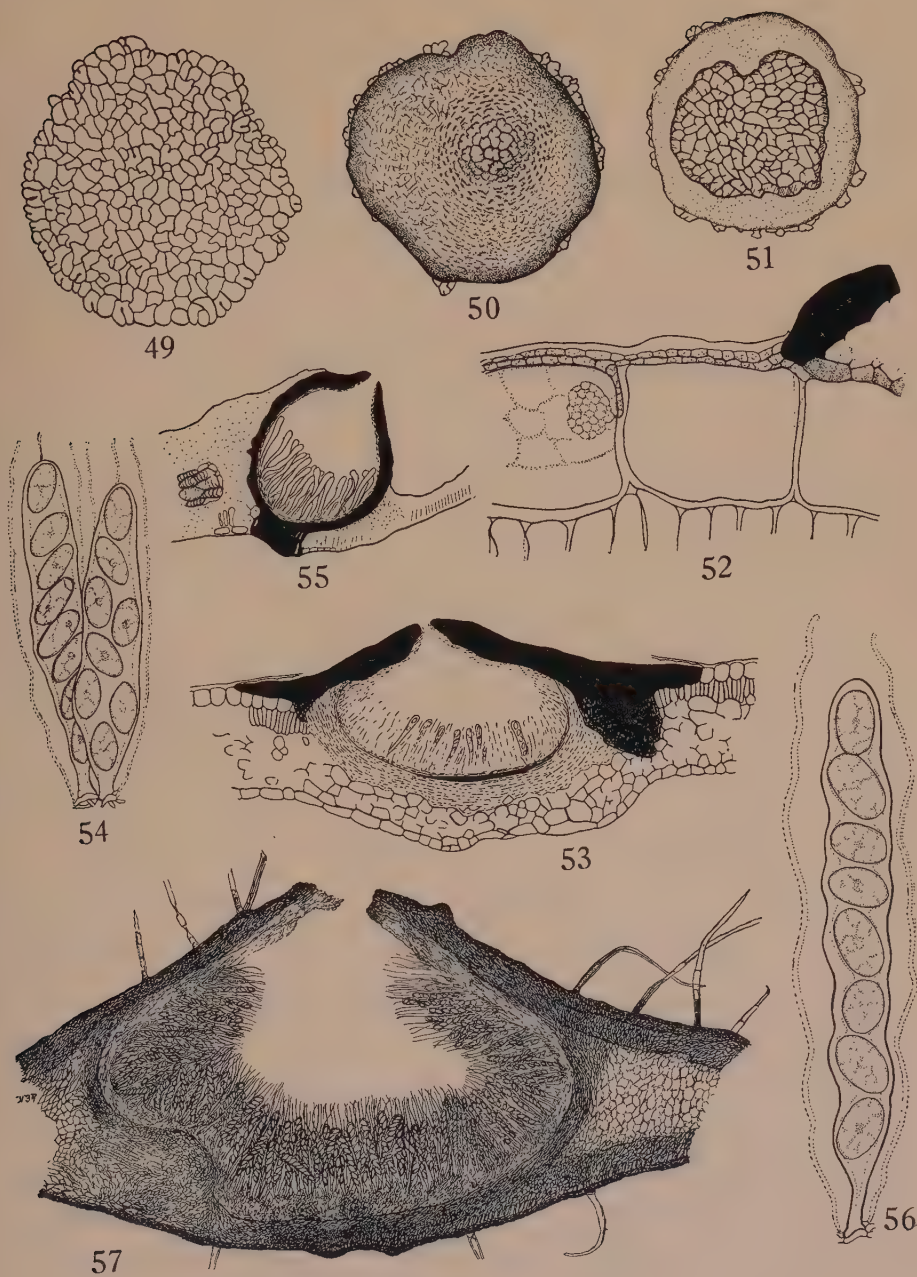
- Fig. 53. Drawing showing locule, stroma, ostiole, clypeus.  
Fig. 54. An ascus and spores.

Figs. 55, 56, *Phyllachora ambrosiae*.

- Fig. 55. Drawing of a stroma and locule.  
Fig. 56. An ascus, spores, and paraphyses.

Fig. 57, *Phyllachora casimiroae*.

- Fig. 57. Cross section of perithecium, showing asci and paraphyses on the hyaline mycelium, surrounded by the darker mycelial layer.





## PLATE VIII

## Explanation of PLATE VIII

Fig. 58, *Phyllachora casimiroae*.

Fig. 58. Asci, spores and paraphyses.

Fig. 59, *Phyllachora icacoreae*.

Fig. 59. Drawing showing stromata and locules.

Fig. 60, *Phyllachora meibomiaae*.

Fig. 60. Drawing of a section through a stroma showing locules and clypeus.

Figs. 61, 62a, 62b, *Phyllachora picramniae*.

Fig. 61. A section showing locules and stroma.

Fig. 62a. Ascus.

Fig. 62b. Spores.

Figs. 63-65, *Phyllachora trophis*.

Fig. 63. Conidial stroma, locules, epidermal stroma.

Fig. 64. Detail of conidiophores and conidia.

Fig. 65. Ascigerous stroma, locule, and clypei.

Fig. 66, *Phyllachorella schistocarphae*.

Fig. 66. Drawing showing epidermal clypeus, subepidermal stroma, locule, border, asci.

Figs. 67, 68, *Phaeodothis costaricensis*.

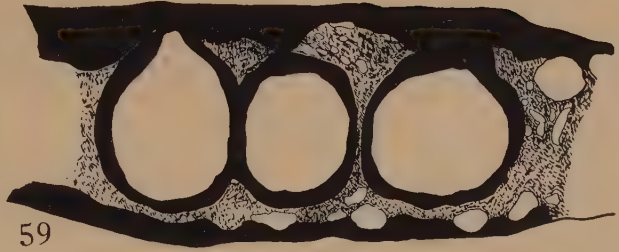
Fig. 67. Showing two regions of stroma and the conidial locules.

Fig. 68. Ascus and ascosphores.





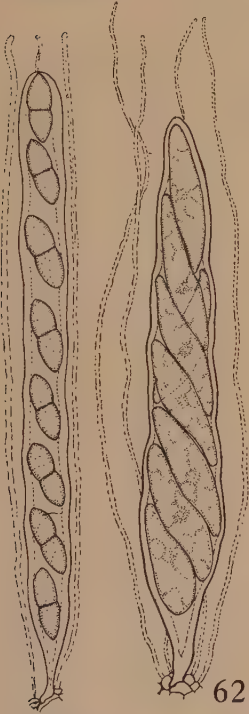
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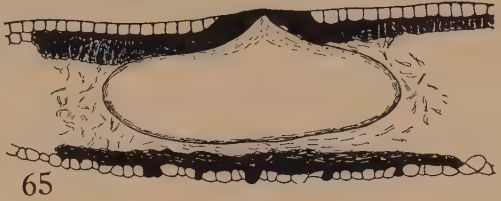
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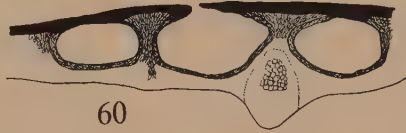
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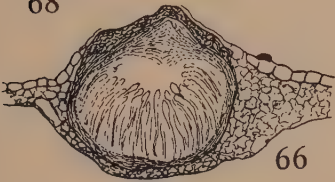
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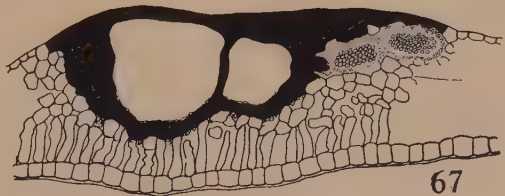
62b



63



66



67



## PLATE IX

## Explanation of PLATE IX

Figs. 69-71b, *Ophiodothella panamensis*.

- Fig. 69. Section of a stroma showing upper and lower clypeus, stroma in the mesophyll and epidermis; locules.  
Fig. 70. Detail of stroma showing dothideoid character, locule border, and epidermal clypeus.  
Fig. 71a. Spores.  
Fig. 71b. Ascus.

Fig. 72, *Haplothecium dioscoreae*.

- Fig. 72. Ascus and spores.

Fig. 73, *Pycnidiostroma eugeniae*.

- Fig. 73. General sketch to show location of the pycnidial locules in the leaf.

Fig. 74, *Othiella fourcroyae*.

- Fig. 74. Asci showing septation, and spores.

Fig. 75, *Physalospora cestri*.

- Fig. 75. A perithecium in a leaf showing locule border and clypeus.

Fig. 76, *Didymella eupatorii*.

- Fig. 76. Showing rostrum, also a conidial cavity.







## PLATE X

## Explanation of PLATE X

Fig. 77, *Didymella eupatorii*.

Fig. 77. A stroma with several locules, one showing the ostiole.

Figs. 78-80, *Mazzantia arundinellae*.

Fig. 78. Mycelium within the epidermal cells as seen from surface view.

Fig. 79a. Diagram (transverse) showing the stroma in the tissues; rind, hyaline mesastroma, locules.

Fig. 79b. Longitudinal section showing the same features.

Fig. 80. Detail drawing showing character of the rind and mesostroma in the host cells.

Figs. 81-83, *Phaeopeltosphaeria panamensis*.

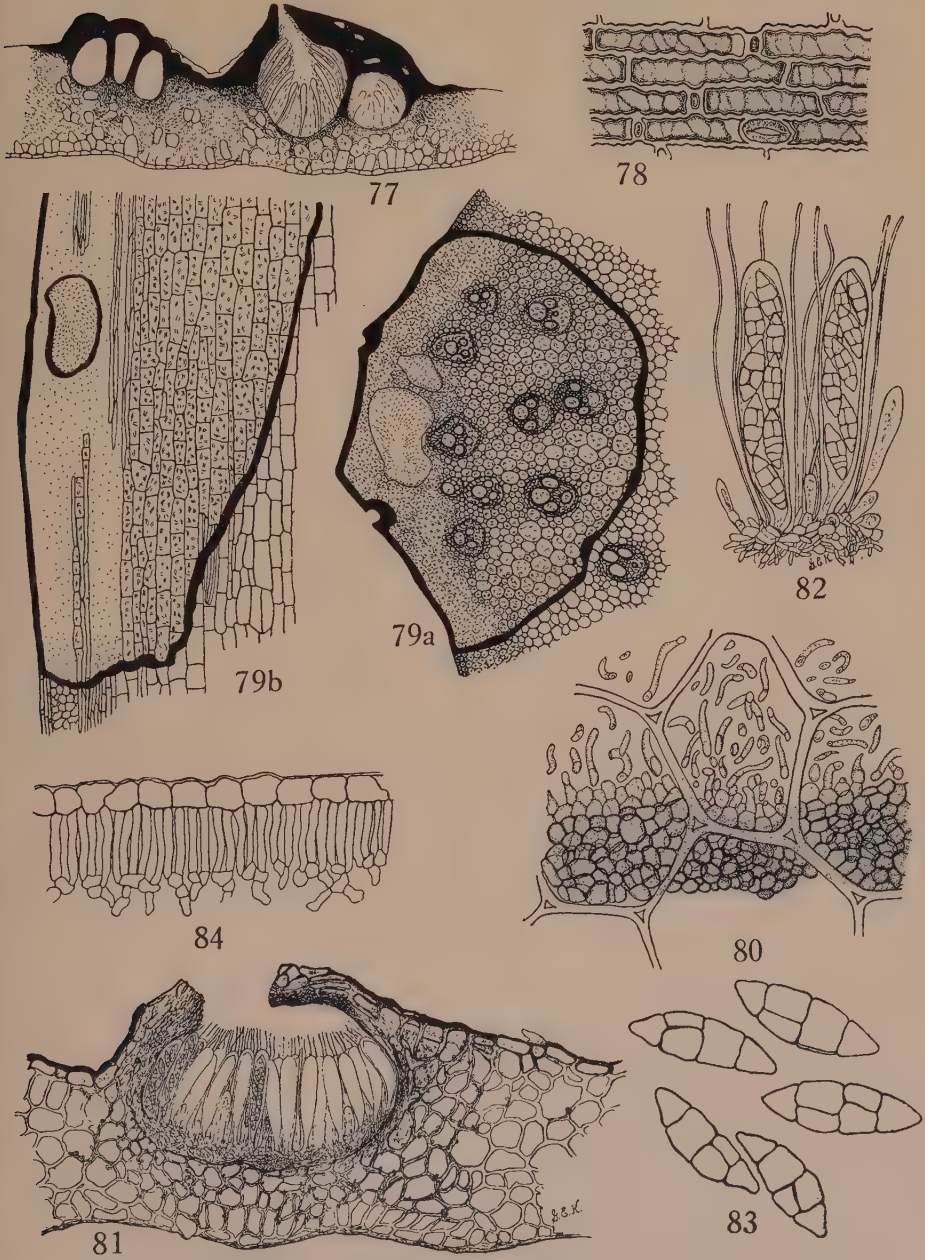
Fig. 81. Cross section of a perithecium showing the structure of the clypeus.

Fig. 82. Asci and paraphyses.

Fig. 83. Spores.

Figs. 84, *Phyllosticta coffeicola*.

Fig. 84. Section showing healthy coffee leaf, thick epidermis.







## PLATE XI

## Explanation of PLATE XI

Fig. 85, *Phyllosticta coffeicola*.

Fig. 85. Drawing showing pycnidia, one merely subcuticular and other in the palisade tissue.

Fig. 86, *Botryodiplodia* sp.

Fig. 86. Conidia, conidiophores and paraphyses.

Fig. 87, *Septoria cavendishiae*.

Fig. 87. Section showing relation of pycnidium to host tissue.

Fig. 88, *Stilbella proliferans*.

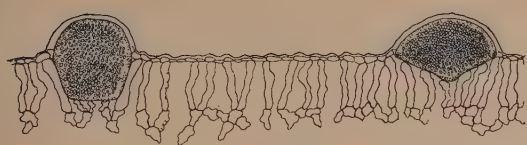
Fig. 88. Coremia showing mode of branching.

Figs. 89-91, *Scenomyces parplexans*.

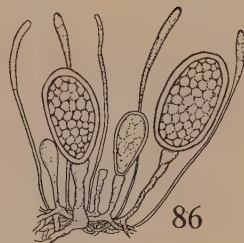
Fig. 89. The origin of a perithecium.

Fig. 90. Detail of a portion of the above.

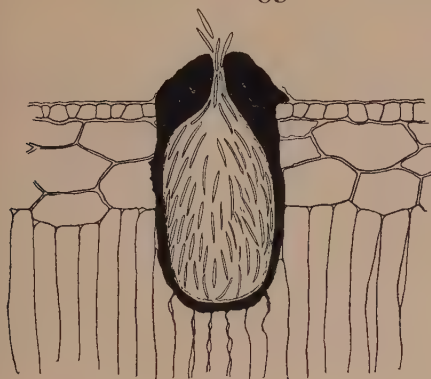
Fig. 91. A perithecium (?) in section.



85



86



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89



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91



## PLATE XII



## Explanation of PLATE XII

Figs. 92-95, *Tryblidiella rufula*.

- Fig. 92. Photograph showing ascigerous disks on the twig.  
Fig. 93. Same as Fig. 92, more enlarged.  
Fig. 94. Same as Fig. 92, but disks more open.  
Fig. 95. Photomicrograph of a disk in section.

## PLATE XIII

## Explanation of PLATE XIII

Figs. 96, 97, *AcrospERMUM foliicolum*.

Fig. 96. Showing habit on diseased leaves.

Fig. 97. Photomicrograph of perithecia.

Fig. 98. *Pseudoparodiella vERNONIAE*.

Fig. 98. Photograph of leaves showing colonies. Largest leaf 13 cm. long.

Fig. 99, *Dimeriellopsis COSTARICENSIS*.

Fig. 99. Photomicrograph showing perithecia and setae.

Fig. 100, *Dimerina DODONAEAE*.

Fig. 100. Photomicrograph of a group of perithecia.

## PLATE XIV

## Explanation of PLATE XIV

Figs. 101, 102, *Polystomella costaricensis*.

Fig. 101. Photograph of a leaf showing stromata.

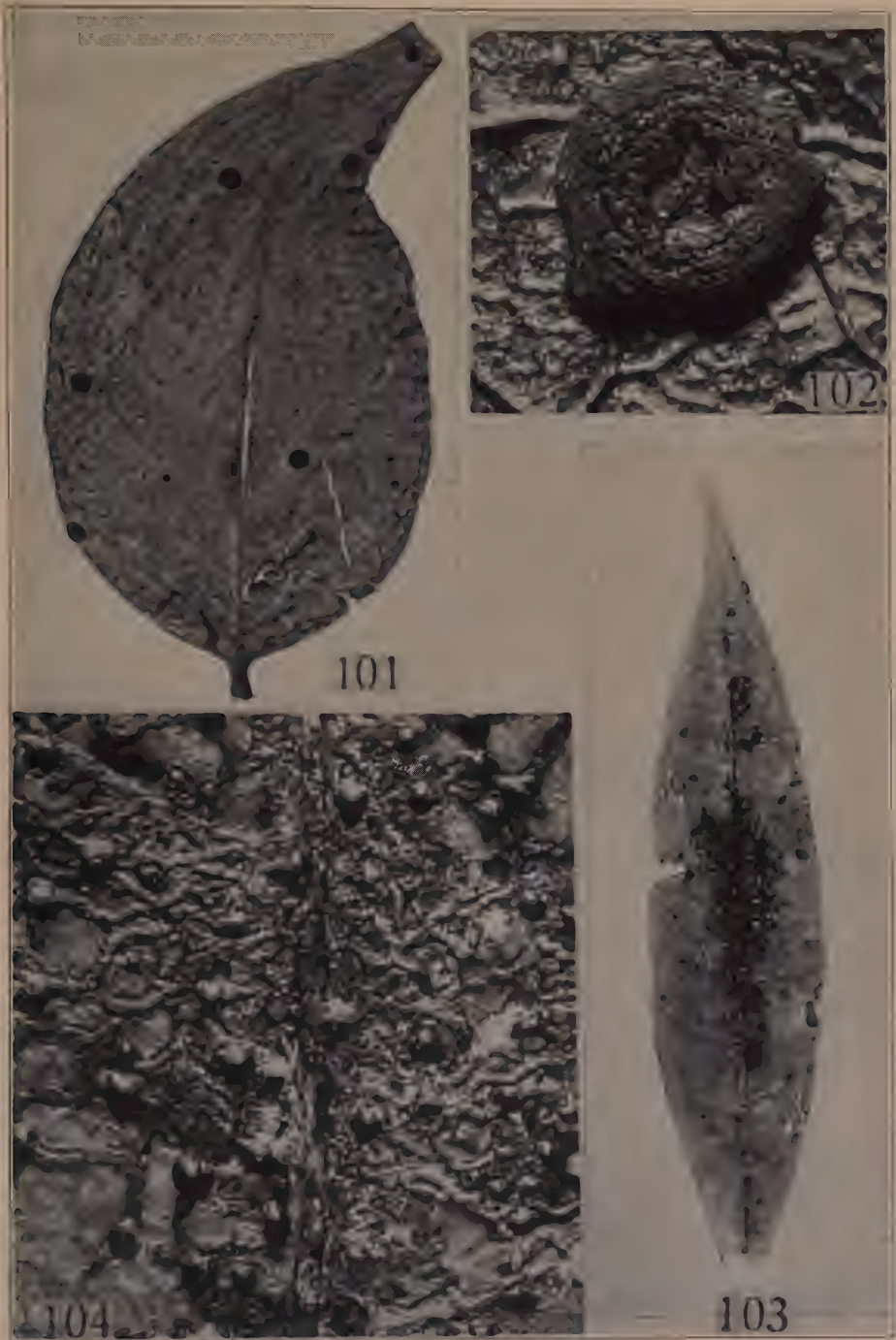
Fig. 102. Photograph of a stroma enlarged.

Figs. 103, 104, *Rheumatopeltis querci*.

Fig. 103. Photograph of a leaf showing thallus.

Fig. 104. Photograph of a spot showing the strap-shaped bands and the loculiferous stromata.







## PLATE XV

## Explanation of PLATE XV

Fig. 105, *Hyperus costaricensis*.

Fig. 105. Photograph of a group of perithecia.

Fig. 106, *Trabutia xylosmae*.

Fig. 106. Photograph of leaf showing stromata. Leaf 45 mm. long.

Fig. 107, *Hypostigma polyadelphe*.

Fig. 107. Photomicrograph showing a group of perithecia.

Fig. 108, *Catacouma costaricensis*.

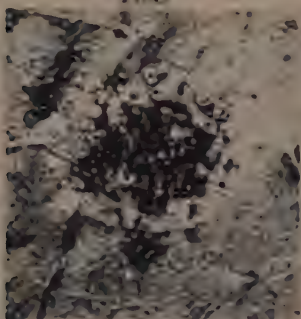
Fig. 108. Photograph showing distribution of the stromata on the leaf. Actual length of leaf 10.5 cm.

Fig. 109, *Catacouma zanthoxyli*.

Fig. 109. Photograph of a leaf showing groups of stromata. Actual length of leaf 93 mm.



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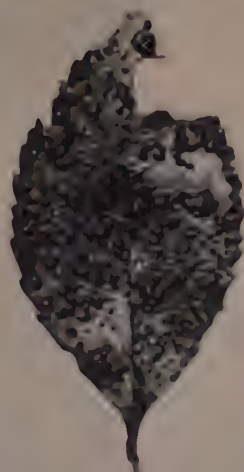
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108



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## PLATE XVI



## PLATE XVII

## Explanation of PLATE XVII

Fig. 116, *Phyllachorella schistocarphae*.

Fig. 116. Photograph showing grouping of the punctiform stromata.

Fig. 117, 118, *Pycnidiostroma eugeniae*.

Fig. 117. Photograph showing stromata on leaf.

Fig. 118. Photomicrograph showing a single stroma with the row of pycnidial locules around the edge.

Fig. 119, *Othiella fourcroyae*.

Fig. 119. Photomicrograph showing groups of perithecia.

Fig. 120, *Mazzantia arundinellae*.

Fig. 120. Photograph of a portion of culm showing stromata.

Fig. 121, *Phyllachora picramniae*.

Fig. 121. Photograph of leaves showing stromata.







## PLATE XVIII

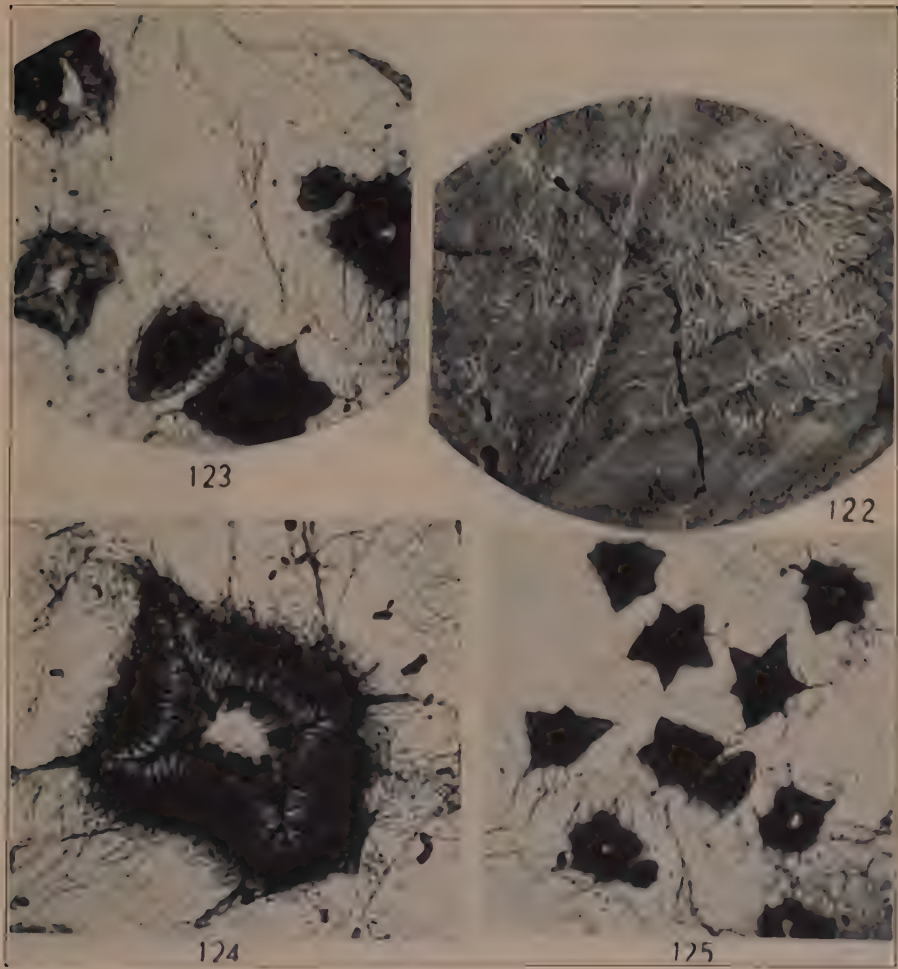
## Explanation of PLATE XVIII

Fig. 122, *Phyllosticta coffeicola*.

Fig. 122. Photomicrograph showing radiations on surface of diseased spot.

Figs. 123, 124, 125, *Scenomyces perplexans*.

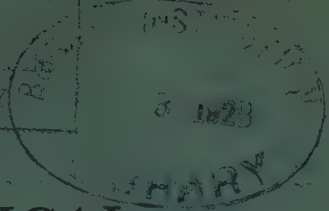
Figs. 123, 124, 125. Photomicrographs of perithecia showing various numbers of rays.







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# THE STRUCTURE AND DEVELOPMENT OF CORALLOBOTHRIUM

With Descriptions of Two New Fish Tapeworms

WITH FIVE PLATES

BY

HIRAM ELI ESSEX

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward  
No. 323



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## INTRODUCTION

Representatives of the genus *Corallobothrium* from American fish have never been described. Marshall and Gilbert (1905) report two members of this genus taken from *Ameiurus melas* (black bullhead) caught in the lakes at Madison, Wisconsin. La Rue (1914) refers to an undescribed species of *Corallobothrium* encysted in the livers of *A. melas* and *A. nebulosus* (common bullhead) from the Illinois River. Ward (1918) noted the presence of a species of *Corallobothrium* in *Ictalurus punctatus* (channel-cat) at Milford, Nebraska. Aside from these incidental references, the American literature contains no information on this interesting group of fish tapeworms.

The acquaintance of the writer with these cestodes began during the summer of 1925 while a survey of the parasites of fish from the rivers and lakes in the upper Mississippi and Missouri basin was in progress (Essex and Hunter, 1926). At that time cestodes belonging to *Corallobothrium* were found in the following hosts: *Ameiurus melas*, *Leptops olivaris* (mud-cat), and *Ictalurus punctatus*.

At the suggestion of Dr. Henry B. Ward an intensive study was begun in the spring of 1926 on the species of *Corallobothrium* infesting *I. punctatus*. As the investigation progressed it came to assume three distinct phases: (1) taxonomy and morphology; (2) seasonal occurrence; (3) life-cycle. It was discovered that two new species of *Corallobothrium* were represented in my collections. These two species are described and named in the present paper. No work having been reported previously on the seasonal occurrence of any fish tapeworm in America, an effort was made to obtain all possible information on this phase of the problem. This study has shed some light on the biological relations between the parasites and their hosts. Up to this time only a few experimental investigations on the life-cycle of fish cestodes have been reported by European workers and none whatever by workers in America. Since such studies are of especial biological significance, and since complete information on the developmental history of fish parasites is of great assistance to fish culturists in their efforts to combat parasitic diseases among fish, all data that I have secured on this phase of the investigation are presented in this paper.

My most sincere thanks are extended to Professor Ward for his inspiration, guidance and helpful criticism in this work. I am deeply grateful for the use of the zoological laboratories of Rockford College which were made available to me, during the summer of 1926, through the



kindness of Dr. Ruth Marshall and the generosity of the college authorities. I also acknowledge here the invaluable assistance rendered by Dr. David H. Thompson of the Illinois Natural History Survey, who furnished me several shipments of catfish for examination. Thanks are also due Mr. R. E. Richardson for the identification of minnows and for a collection of parasites from *Ictalurus punctatus*, and to Dr. S. A. Forbes for the use of unpublished data on the food of *I. punctatus* collected by the Illinois Natural History Survey.

#### MATERIAL AND METHODS

The parasites were killed in corrosive sublimate, Bouin's solution and 4 per cent formol. The first two gave good results, but specimens killed in formol were difficult to stain. Ehrlich's or Delafield's hematoxylin was used for totos and sections. Counterstaining was done with eosin or orange G.

Collection of the adult cestodes offers no difficulties, but it is a long and tedious struggle to find the smallest larval forms. A method was developed whereby plerocercoids which measured only 0.25 mm long could be collected with a saving of time and effort. Briefly stated, the procedure is as follows: (1) large parasites and particles of debris are removed; (2) remainder of intestinal contents scraped into quart jar of water and shaken thoroughly; (3) the mass is strained through a small plankton net; (4) the plankton net placed under faucet, running water allowed to play on contents until all possible material is washed through the net; (5) the residue is turned into a watchglass and examined under a binocular. This method is equally successful in collecting small trematodes.

A rapid method of reconstruction was developed in connection with the work on these cestodes. A plate of glass one foot square was placed under the camera lucida. With a wax pencil the structure to be reconstructed from a given section was traced on the glass. With plasticene the tracings were modeled. The next section was then oriented according to guide lines and the required tracings made from it. By means of blocks of plasticene the structures modeled from the second, third, and later sections were placed according to scale above those previously modeled. When completed, the organs were represented in three dimensions and in their proper relation. This method was employed in making the models represented by figures 39 and 41.

### THE GENUS CORALLOBOTHRUM

The genus *Corallobothrium* was created by Fritsch in 1886 to accommodate a species of cestode from *Malapterurus electricus*, an electric catfish of Egypt. Because of the resemblance of the scolex to the structure of an *Oculina*-like coral, he named the parasite *Corallobothrium* and called the species *C. solidum*. It was his opinion that this genus represented a connecting link between the Bothriocephalan and Taenian cestodes. He gave the following diagnosis for the genus: "Caput bothrio uno terminali, fere plano, ovali lateribus attenuatis, superficie et margine crispo. Acetabula quattuor cruciatim posita, in bothrii medio profunde inserta. Collum nullum. Corpus articulatum, depressum, subaequale vel retrorsum angustatum. Organa genitalia typica, orificia marginalia involuta." Fritsch says that the form of the scolex recalls that of *Caryophyllaeus*, "nur ist die Sauggrube in ihrer ovalen nach beiden Seiten leicht verschmälerten Gestalt, viel regelmässiger gebildet"; that the acetabular suckers are entirely obscured by the folds of the scolex and are revealed only in sections. The suckers agree in structure and arrangement with those of *Taenia*; the character of the whole body is strikingly solid and strong.

No other species was referred to the genus *Corallobothrium* before the work of Ruggenbach (1896), who described a cestode from *Pimelodus pati*, a siluroid of Paraguay. This parasite was designated as *Corallobothrium lobosum*. Fuhrmann (1916) redescribed this form and gave a short redescription of *C. solidum*. On the basis of the cortical arrangement of the testes and vitellaria he removed *C. lobosum* from the genus *Corallobothrium* and created for it a new genus, namely, *Rudolphiella*. Later Fuhrmann and Baer (1925) reduced *Rudolphiella* to synonymy, and placed *R. lobosa* in the genus *Ephedrocephalus*.

Braun (1895) accepts the genus *Corallobothrium* and to Fritsch's diagnosis adds that neither hooks nor spines are present; that excretory vessels have secondary openings in the proglottids; and that the hosts are tropical or subtropical bony-fish. La Rue (1914) adds to Braun's diagnosis that the folds and lappets of the scolex may enclose the suckers as in a corolla and that no rostellum is present. He omits the secondary openings of the excretory system, given by Braun, and gives the habitat as the intestinal tract of the Siluridae.

The validity of the genus *Corallobothrium* was never questioned until the appearance of two papers by Woodland (1925, 1925a) in which he proposes to delete such genera as *Corallobothrium*, *Choanoscolex*,

*Acanthotaenia* and *Gangesia* and make them synonyms of *Proteocephalus* because they were founded on scolex characteristics. This author regards such characters as of specific value only, and proposes that the various arrangements of the reproductive organs with reference to the inner longitudinal muscle sheath shall constitute the bases for the designation of genera. In Woodland's opinion the scolex characters are of secondary importance as compared to the structure of the proglottids. However, if the early development of the cestodes is accepted as a guide in determining the order of sequence<sup>3</sup> which is followed in arriving at the adult organization, and if those structures which appear first in the development of the individual are considered as having arisen first in the phylogeny of the group, then the scolex must be acknowledged as one of the most fundamental structures of the adult organism. In the development of *Taenia* and related groups, the scolex and a more or less indifferent neck are the only adult structures found in the cysticercus, and from them arise all other adult organs. In the development of the two new species described in this paper the scolex is likewise the first adult structure to appear, being differentiated at the end of 10 to 12 days development. When considered from this point of view, there is certainly sufficient reason for attaching generic value to the character of the scolex. Fuhrmann (1916) doubtless recognized this when he created a separate genus for *Goezeella siluri* instead of referring it to the genus *Monticellia*; the only essential difference between the two genera being that the former possesses a scolex of the *Corallobothrium* type. Furthermore, the scolex has long been used by helminthologists as a generic character, and to discard it now would result in more confusion of the nomenclature than seems to be justified. A recent publication by Stiles and Hassell (1926) contains the following statement: "The genus *Taenia*, in its modern concept, can be subdivided into at least three groups to which either subgeneric or generic rank may be given (according to one's personal point of view in respect to generic values)." A key follows in which the genera *Taenia*, *Hydatigera* and *Taeniarhynchus* are separated entirely on the basis of the scolex while *Taenia* and *Taeniarhynchus* are separated on the nature of the rostellum alone.

Since the characters which constitute a genus are considered largely a matter of personal viewpoint, Woodland is hardly justified in deleting genera which have been accepted previously by the leading workers in helminthology because, from his point of view, he does not regard the characters on which those genera were founded as of generic value. Therefore, I have followed Braun, Fuhrmann and others in accepting the genus *Corallobothrium* and the two new species described in this paper have been referred to that genus.



Corallobothrium is closely related to the genus *Proteocephalus*. The internal organization of the two genera is very similar. The scolex, however, is so distinctive that species belonging to the two genera can be separated by an examination of the scolex alone. Another character by which the species of *Corallobothrium*, which I have studied, may be separated from those of *Proteocephalus*, is in the position of the vagina with reference to the cirrus-pouch. In *Corallobothrium giganteum* and *C. fimbriatum*, the vagina in successive segments varies and may be either anterior or posterior to the cirrus-pouch. The descriptions of *C. solidum* are silent on this point, but if this condition is true of it also, there exist two distinct points of difference, scolex and position of vagina, between the species of *Corallobothrium* and *Proteocephalus*. Regarding the latter La Rue (1914) makes the following statement: "In *Proteocephalus* the vagina is usually anterior to the cirrus-pouch although there are a few species in which it is regularly posterior." Thus in the species of *Proteocephalus* the position of the vagina with regard to the cirrus-pouch is constant, while in the species of *Corallobothrium* it is inconstant.

The genus *Corallobothrium* may be defined as follows: With characters of family. Scolex bears four suckers situated on anterior surface surrounded by many irregular folds and lappets of tissue. Rostellum, hooks and spines absent. Neck broad, short. Vagina inconstant in position, anterior or posterior to cirrus-pouch. Habitat: In Siluridae. Type species: *Corallobothrium solidum* Fritsch.

#### CORALLOBOTHRIUM GIGANTEUM NOV. SPEC.

In life these cestodes are milky-white in color. The scolex is usually attached in the region of the duodenum and the proglottids of a mature specimen may extend almost to the posterior limit of the intestinal tract of the host. They are strongly contractile and may draw themselves up to less than half the fully extended length. The strobilization is indistinct except in the posterior portion of the chain. The body surface is excessively wrinkled in this species as is true of the whole genus. The proglottids are so firmly joined that considerable force is required to tear them apart. The proglottid number varies from 150 to 300 or more.

Among seventy-five adult individuals before fixation, 60 cm was the greatest length observed. After fixation the longest individual was 44 cm. The usual length of preserved specimens ranges between 15 and 30 cm. In the largest living individuals mature proglottids are about 3 mm long by 2.5 mm wide; ripe proglottids 4 to 8 mm long by 1 to 0.5 mm wide, according to contraction. In the largest fixed specimen (44 cm) which was not fully extended, immature proglottids were from 0.25 to 0.75 mm long by 5 mm wide to 1 mm long by 3.5 mm wide; mature proglottids from 1 mm long by 3.5 wide to 2 mm long by 2.25 mm wide; ripe proglottids

from 2 mm long by 2.25 mm wide to 5 mm long by 1 mm wide. In an alcoholic specimen 22 cm long, containing about 225 proglottids, 3 cm from the scolex, the proglottids are about 0.25 mm long by 2.5 to 2.75 mm wide; about 8 cm from the scolex they are 1 to 1.3 mm long by 2 to 1.5 mm wide; the last 20 proglottids measure from 1.5 to 2 mm long by 1 to 0.5 mm wide. In four toto preparations of sexually mature specimens which measure from 5 to 15 cm in length, immature proglottids are 0.10 to 0.84 mm long by 1.51 to 3.10 mm wide; mature proglottids 1 to 2.2 mm long by 1.3 to 1.89 mm wide; ripe proglottids 1.53 to 3.46 mm long by 0.73 to 1.15 mm wide. The segments in the anterior portion are always wider than long, but proceeding posteriad the length gradually increases at the expense of the width and the posterior proglottids of the chain are much longer than wide, the ratio begin from 2:1 to 8:1 (Figs 6, 26). The shape of the cestode in toto recalls that of a whip.

The form of the scolex is highly variable owing to different states of contraction. It may be globose (Fig. 15), quasi-conical (Fig. 5), quadrate (Fig. 2), or it may in a measure resemble the head of *C. fimbriatum* (Figs. 10, 11). In living specimens it varies from 1 to 2.75 mm in diameter. In six alcoholic specimens, which are representative of the adult worms, the scolex measures from 1 to 2.16 mm wide. The ratio of the width to the length varies from about 1:1 to 2:1. Among four toto mounts the diameter is 1.47 to 1.68 mm and the length is 0.9 to 1.5 mm. The dorso-ventral dimension is usually slightly less than the transverse diameter. The four strongly muscular suckers, which are directed anteriorly, are largely concealed beneath a heavy fold of the cortex. From this fold project a large number of ridges and a few finger-like processes. The folds and lappets are much less pronounced than those of *C. fimbriatum* and *C. solidum* (Figs. 5, 10, 15). At times the suckers are drawn in and covered entirely (Fig. 11). When this occurs the scolex is drawn back into the neck region (Fig. 10). This gives the anterior extremity a flattened appearance. When the scolex is fully extended, the anterior extremity is rounded and the bluntly pointed apex projects from the center (Fig. 5). There is no rostellum or rudiment of a fifth sucker revealed in five sets of frontal and one set of transverse sections.

The suckers, which measure from 0.45 to 0.59 mm wide and from 0.53 to 0.59 mm long, vary in shape according to their contraction. In some specimens they are nearly spherical while in others they are longer than wide. One series of frontal sections shows each pair lying with their inner margins touching in the posterior portions while the anterior portions are quite widely separated, each one making an angle of about 30 degrees with the longitudinal axis of the worm (Fig. 33). In another series of frontal sections, each pair of suckers is separated by a distance of about 0.10 mm and they are directed anteriorly so that their longi-



tudinal axes are parallel with that of the scolex (Fig. 37). The first series was made from a specimen that was fairly well extended, the second from one that was much more contracted. The width of the openings varies from 0.10 to 0.19 mm and the length of the cavity may be as much as 0.33 mm.

At the apex of the suckers, surrounding the inner half of the opening, is a massive set of muscle bands which pass from the margin of the opening on one side in a circular course to the opposite side of the opening. They form a semi-circle about the apex of the suckers. In transections they appear as shown in figure 18; in frontal sections they are about 0.20 mm in diameter and resemble knobs (Fig. 37). Woodland (1925a) has reported a similar structure for the suckers of *Marsypocephalus rectangularis*. This structure functions as a sphincter and, as Woodland has suggested, doubtless aids in prehension. It was noted, in dealing with the living *C. giganteum* that they were detached with great difficulty when the scolex of one fastened itself upon another individual.

Besides the sphincter, each sucker is encircled by a very compact band of muscle fibers  $16\mu$  thick at the center. These fibers may be divided into two groups: those which surround the sucker in the frontal, and those which surround it in the sagittal plane. Within this band appears a layer of muscle fibers about 0.30 mm thick in the center. These are much less compact in their arrangement and all of them extend from the periphery of the sucker to the lining of the cavity. Lining the cavity of the sucker is a layer of cuticula which measures from 3 to  $4\mu$  in thickness.

Anterior to the suckers there is a rhomboid of muscle fibers (Fig. 35) and from the margins of the suckers many muscle fibers proceed into the neck region (Fig. 37). Posterior to the rhomboid of muscle fibers is a transverse cross of fibers. At the level of the sphincter a set of fibers pass from one sucker to the next (Fig. 18). Transverse sections through the posterior portions of the suckers show two bundles of muscle fibers, one arising from each of the inner margins of the suckers. These bundles pass diagonally to a member of the opposite pair. In their course they cross each other near the median line to form an eight-rayed cross or star (Fig. 28).

The neck in one set of frontal sections is about 1.60 mm long and 1.36 mm wide. It is easily recognized in frontal sections but it is not evident in much contracted totos. There is frequently very little constriction immediately posterior to the scolex. Thus the diameter of the neck region, when a specimen is much contracted, may equal that of the scolex (Figs. 10, 16, 37).

The cuticula, which varies from 4 to  $9\mu$  in thickness, is composed of two layers. A thin, more deeply staining layer about  $1\mu$  thick, covers the surface. Beneath it is a thicker, less deeply staining stratum at the inner

margin of which is found the very thin basement membrane, less than  $1\mu$  thick. Beneath this is a layer of circular muscles about  $3\mu$  thick. There are longitudinal muscle fibers just below the circular muscles. The former are interwoven with the outer ends of the spindle-shaped subcuticular cells which form a phalanx beneath the subcuticular muscles. These cells constitute a layer about 0.03 mm thick. They possess large nuclei which vary in shape, some of them being spherical and others elliptical. Each cell is drawn out into a fine process which can be followed as far as the basement membrane.

In the strobila the inner longitudinal muscle sheath is exceptionally well developed. In mature proglottids it measures from 0.05 to 0.07 mm thick. The fibers are arranged in irregularly shaped bundles. Just within this layer appears a band of inner circular fibers. This band constitutes a stratum from 6 to  $16\mu$  thick, which encircles the medullary parenchyma. In immature segments transverse fibers are quite numerous. Passing through the medullary region, as many as 60 bands of dorso-ventral fibers were counted in a single section of a mature proglottid.

The nervous system consists of a ring and two nerve trunks. The former is situated in the median region of the scolex at the level of the apices of the suckers. In transections it has the form of a cross, the rays of which project between the suckers (Fig. 35). Its greatest diameter in adults is from 0.33 to 0.40 mm. Arising from the lateral portions of the ring two trunks, which measure from 35 to  $40\mu$  in diameter, pass off parallel to the ascending excretory vessel and follow a course between the dorsal and ventral pairs of suckers along the inner margin of the longitudinal muscle layer (Fig. 30). In the scolex and throughout the proglottids these nerve trunks maintain the same relation to the inner longitudinal muscle sheath, and their diameter varies but little at any point in the chain.

The excretory tubules are very prominent in sections of this species. Four principal tubules are easily seen in sections of proglottids which are immature. When the reproductive organs are fully developed the excretory system is so crowded that at times it is difficult to distinguish it clearly. The four main longitudinal trunks are located in the lateral regions of the medullary parenchyma roughly parallel to the longitudinal nerve trunk of each side, the descending lying nearer the center than the ascending vessels.

The ascending tubules, which measure from 12 to  $18\mu$  in diameter, lie only 5 to  $15\mu$  from the nerve trunk, both in the neck region and in the immature proglottids. In these regions they follow a straight course with only slight deviations. The descending tubules are much larger in the regions just named, as they measure from 24 to  $40\mu$ . Their course is much more tortuous and their position with reference to the nerve trunk is much less definite.

The structure of the ascending and descending trunks is very different. Transections of the former show a heavy wall of hyaline material about  $1\mu$  thick surrounded by what appears to be a single layer of muscle fibers. Also the parenchymal cells are compactly arranged about these tubules (Fig. 40). The descending trunks lack the hyaline wall and also the layer of muscle fibers, and they are surrounded by a less compact arrangement of the parenchymal cells.

In a larval specimen about 4 mm long, cut in transverse section, the ascending trunks arise 0.14 mm from the posterior end of the individual where they measure from 2 to  $5\mu$  in diameter. They are found in the lateral medullary parenchyma. As they proceed anteriorly they increase slightly, measuring 8 to  $10\mu$  at a point about 0.8 mm from the scolex. As they enter the scolex they measure about  $8\mu$  in diameter. Upon reaching the scolex they pass laterally between the suckers and the longitudinal muscle layer of the scolex, following the outer margins of the suckers until the anterior level of the latter is reached, when they proceed inward toward the median line where they follow a tortuous course between the suckers before uniting with the descending trunks.

Branches of the descending trunks are more numerous in the central region of the scolex. The apex is ramified with both ascending and descending branches, but about the bases of the suckers there occur numerous coils of the descending tubules. Upon reaching the neck region, the main vessels proceed laterally, the ascending running dorsal and the descending ventral to the nerve trunk. In the neck the ascending trunks measure about 0.02 mm, or twice the diameter of the ascending ones. Throughout the length of the individual there is little difference in the diameter of the descending tubules since they measure from 20 to  $25\mu$  in the posterior region. There are no cross trunks apparent between the vessels of the same or opposite sides in the parasites at this stage of development. Furthermore, they follow practically a straight course throughout. About 0.08 mm from the posterior end, the two descending trunks empty into an excretory bladder. Just below the point of union with the descending tubules, the bladder measures  $20\mu$  dorso-ventrally and  $27\mu$  transversely. It narrows posteriorly and empties through a small duct at the extreme posterior end of the individual.

Frontal sections were made of a strongly contracted individual, about 15 mm long, in which a large number of proglottids had been differentiated. Here the excretory system is much more highly developed than in the individual just discussed. The position of the ascending and descending trunks with reference to each other has been slightly altered. At this stage they are parallel in a horizontal plane, with the ascending trunk more lateral or nearer the longitudinal nerve on each side. The diameter of the ascending is less than that of the descending trunks throughout



their extent. Both are more or less coiled in this individual. With the differentiation of proglottids an addition to the descending system has occurred. At the posterior limit of each proglottid is found a cross-trunk which in many instances equals in diameter the descending tubules. Also a small duct,  $8\mu$  in diameter, arises near the confluence of the descending and cross trunks. This passes to the postero-lateral margin of the proglottids and empties to the outside through a small duct and pore (Figs. 34, 38). These same features are found also in the fully mature segments, but owing to the pressure of the reproductive organs they are more difficult to distinguish. The excretory system of this species agrees in all essential features with the description of Riggenbach (1896) for *Ephedrocephalus lobosus* (= *Corallobothrium lobosum*).

A study of frontal sections of the scolex and strobila in an extended and contracted condition has lead me to the conclusion that this system has more than an excretory function. When the scolex and strobila are contracted, the vessels are greatly diminished (Figs. 16 and 38). When the opposite is the case, the vessels are much distended (Figs. 21 and 34). This suggests the probability that the excretory vessels aid in the extension of the scolex and strobila.

#### *Reproductive Organs*

A common genital sinus, which measures about  $64\mu$  in diameter, occurs on the lateral margin of the proglottid from one-quarter to one-half the proglottid length behind the anterior margin. The usual position is within the anterior one-quarter of the proglottid. It is irregularly alternate in successive segments. The cortical wall surrounding the sinus protrudes sufficiently to be seen with the naked eye in toto mounts. This constitutes a genital papilla. The character and arrangement of the reproductive organs, for the most part, is identical with that of the other Proteocephalids. Each sexual unit occurs within the inner longitudinal muscle sheath (Fig. 20).

The male system will be considered first. The testes vary considerably in shape. Some of them are almost spherical, others pear-shaped, but the majority are elliptical. They measure from 0.05 mm to 0.08 mm in length, and from 0.03 to 0.06 mm in diameter. The number present in a single proglottid is from 80 to 100. They lie in a continuous field between the vitelline glands, extending from the anterior margin of the proglottid posteriad to the level of the ovary. Between the vitelline glands and the uterus they occur in two or three layers, but dorsal to the uterus only a single layer is present. Vasa efferentia were not observed in any of the preparations. In many sections the vas deferens passed among the testes and often there appeared to be a connection between the walls of the two. This relation could not be established for a sufficient number to warrant the statement that such is the usual condition.

At the level of the cirrus the thin-walled vas deferens, which measures from 0.03 to 0.05 mm in diameter, forms a compact mass of 15 to 20 coils that almost completely fill the medullary space between the vitellaria and uterus and extend anteriorly and posteriorly from 0.25 to 0.33 mm. (Figs. 7, 26). In mature proglottids they are usually distended with spermatozoa. At the point of entrance into the cirrus-pouch the vas deferens ends abruptly and at this point the ductus ejaculatorius takes its origin. After describing two or three coils it passes into the cirrus. The duct at the point of entrance into the cirrus-pouch measures about  $16\mu$ . A short distance beyond its point of entrance it doubles in diameter. Upon entering the cirrus it narrows again. Its lumen varies from 8 to  $12\mu$  in diameter. Its structure is almost identical with that of the cirrus.

The cirrus-pouch is usually elongate-oval in shape when the cirrus is inverted, but its form varies when the cirrus is everted. Apparently the extent of protrusion of the cirrus affects the shape of the cirrus-pouch. It assumes a variety of forms in successive segments. Some appear wedge-shaped, while others recall the form of a gourd (Fig. 7, 26). When the cirrus is inverted, the pouch measures from 0.26 to 0.33 mm long by 0.09 to 0.13 mm in greatest diameter. The wall of the pouch is from 3 to  $5\mu$  in thickness and is composed of longitudinal muscle fibers. Between the wall of the pouch and the cirrus is a loose network of connective tissue fibers with scattered nuclei. Immediately surrounding the cirrus is a compact layer of cells about  $8\mu$  thick. Wagner (1917) in his description of *Protecephalus torulosus* calls a group of cells similarly located, subcuticular cells. Benedict (1900) in his description of *P. filicollis* and *P. ambloplitis* designates them as gland cells.

When the cirrus is inverted it measures from 0.20 to 0.23 mm in length and about 0.02 mm in greatest diameter and about the same at its point of union with the ductus. It is roughly cone-shaped, the base of the cone being adjacent to the genital sinus. In transections the wall of the cirrus shows a series of closely applied folds which almost close the lumen. The inverted cirrus is lined with a cuticular layer that extends to the ductus. Surrounding this layer are found longitudinal and circular muscles. When completely everted the cirrus reaches a length of 0.5 mm. Its diameter just outside the genital sinus is about 0.1 mm, while its distal portion has a diameter of about 0.05 mm (Fig. 17).

In the female system the vagina opens into the genital sinus beside the cirrus in the same horizontal plane. Frontal sections of two individuals showed that the vagina may be either anterior or posterior to the cirrus. In one individual the vagina opened anterior to the cirrus on the right side in 14 proglottids, and on the left side anterior to the cirrus, in 12 proglottids. It opened posterior to the cirrus on the right side in 10 proglottids and posterior to the cirrus on the left side also in 10 proglottids.



In another specimen the relation was as follows: anterior to cirrus, right side, 18; anterior to cirrus, left side, 20; posterior to cirrus, right side, 10; posterior to cirrus, left side, 13. In these two specimens there is a close approach to equality in the dextral and sinistral position, and antero-posterior relation of the vagina and cirrus. For a distance of about 0.10 mm from the sinus the diameter of the vagina may almost equal that of the cirrus, and like the latter has a lining of rather heavy cuticula. A sphincter vaginae is present but weakly developed. At the end of the distance just mentioned the vagina narrows, and from there to the seminal receptacle it measures from 11 to  $24\mu$  and its lumen varies from 6 to  $20\mu$  in diameter. The greater diameter is only reached when the vagina is distended with spermatozoa. Since the vaginal opening may lie either anterior or posterior to the opening of the cirrus, the course of the vagina will vary somewhat. From the level of the genital sinus it may pass anteriorly for a short distance before proceeding toward the median line, or it may run between the coils of the vas deferens in a direct course toward the median line of the segment. At the same time it is directed ventrad. It passes through the ventral region of the medullary cortex for a short distance, then turns dorsally and for the remainder of its course to the seminal receptacle, it lies above the uterus. It is found in this last position throughout about two-thirds of its length. Anterior to the ovarian commissure when the proglottid is much extended, and posterior to it in contracted segments, the vagina widens gradually for about 0.10 mm, then it narrows suddenly, giving rise to a pear-shaped seminal receptacle which equals the width of the vagina at its narrowest point and is about 0.04 mm at its widest portion (Fig. 23). Leading from this structure is a narrow duct, the lower vagina, which joins the oviduct. This portion may be straight (Fig. 23) or coiled (Fig. 39). The position of the duct is dependent upon the contraction of the proglottids. Aside from a cuticular lining for a short distance from the genital sinus, the wall of the vagina is composed of muscle fibers and measures from 3 to  $5\mu$  in thickness. Only longitudinal fibers were distinguished. Like the cirrus, it is surrounded by a layer of gland cells throughout its length.

The bi-lobed ovary lies in the posterior portion of the proglottids. In fully extended ripe proglottids it is H-shaped. The two wings are broad and bluntly rounded posterior to the commissure, but anterior to it they taper to a rather sharp point and measure from 0.86 to 1.32 mm in length. The width of the ovary at the level of the commissure is from 0.33 to 0.46 mm (Figs. 23, 26). In fully extended ripe proglottids the structure of the ovary has a latticed or corded appearance as it is made up of a network of thin-walled tubules which are interwoven with one another. In mature proglottids the lobes of the ovary are much shorter and more compact, measuring from 0.46 to 0.80 mm in length and from 0.75 to 1.06 mm in width at the level of the commissure (Fig. 26).

As revealed by sections, the two lobes lie just beneath the inner longitudinal muscles in the dorsal region of the medullary parenchyma but the commissure dips ventrally. Near the median line, it connects with the muscular oocapt which is spherical in shape and measures about  $20\mu$  in diameter. It is surrounded by a layer of gland cells about  $4\mu$  thick. From the oocapt in mature proglottids the oviduct usually changes direction three or four times before reaching the posterior margin of the segment where it turns laterad and dorsad. Near its lateral limit it empties into the ootype. The greatest diameter of the oviduct is about  $24\mu$ . The lower vagina joins the oviduct at its last bend before the ootype is reached (Fig. 39).

The ootype, which is about the same diameter as the oviduct, passes laterally and dorsally for a short distance and then proceeds anteriorly. Near the anterior level of the vitelline receptacle it empties into the uterine passage. The wall of the ootype is very similar to that of the oviduct. The only striking difference between the two structures is the presence of the shell gland about the former, some cells of which measure  $48\mu$  long by  $16\mu$  wide. The processes of these cells pass into the wall of the ootype.

The uterine passage, which leads from the ootype, measures about  $16\mu$  in diameter. After bending upon itself once or twice it passes dorsal to the vagina and empties into the uterus near the median line at a point near the middle of the proglottid.

In mature proglottids the uterus has a diameter equal to about half the proglottid width. It is separated from the vitellaria on each side and from the dorsal musculature by the testes. It extends from the anterior margin to near the level of the ovarian commissure. It opens to the exterior through two or three uterine pores near the ventral median line. In mature proglottids the uterus possesses from 10 to 15 lateral pouches (Fig. 26). Their beginnings are very distinct in immature proglottids. In fully extended, partially spent proglottids the lateral pouches are relatively greatly reduced, giving the uterus the character of a tube with irregular borders (Fig. 6).

The vitellaria form two columns of a diameter of 0.08 mm which extend from the anterior to the posterior margin of the proglottid. They crowd the longitudinal nerve trunks close to the inner muscle sheath. They are follicular in structure, the follicles emptying into a central tubule. Near the level of the ovarian commissure a duct  $16\mu$  in diameter leads inward from each side. The two unite anterior to the oocapt, forming a common vitelline duct which proceeds posteriorly for about 0.05 mm and then widens to form the vitelline reservoir, which is from 40 to  $56\mu$  long and from 28 to  $36\mu$  wide. From the reservoir a narrow duct leads into the ootype near its point of union with the oviduct (Fig. 39).

## AMPHITYPY

Amphitypy, or complete organ reversal, occurs in the position of all the interovarian organs in successive segments. This condition is not correlated with the position of any of the other organs of the reproductive system. For example, the genital sinus may be on the left margin with the vagina anterior to the cirrus and with the interovarian organs disposed as shown in figure 39. In another segment the genital sinus will be on the right with the vagina posterior to the cirrus and the interovarian organs will be arranged the same as in the figure just cited, or they may be just the reverse. The following data were taken from seven successive segments cut in frontal section.

Genital sinus	Right	Right	Left	Right	Right	Left	Right
Vagina anterior to cirrus	+		+				
Vagina posterior to cirrus		+		+	+	+	+
Oviduct right	+	+	+		+		
Oviduct left				+		+	+
Seminal receptacle right				+		+	+
Seminal receptacle left	+	+	+		+		
Vitelline reservoir right	+	+	+		+		
Vitelline reservoir left				+		+	+

Amphitypy has been observed among the Trematoda by many investigators (Looss, 1902: 789) but I have not discovered any reference to such a condition among the Cestoda.

A description of the living eggs is given later in this paper consequently only the ova within the uteri of sectioned specimens are considered here. The outer egg covering is so variable in amount and so irregular in shape that it is difficult to distinguish in preserved material. The second membrane is spherical and measures from 14 to 19 $\mu$  in diameter. This membrane is closely applied to the oncosphere which measures from 8 to 13 $\mu$  in diameter. The eggs of this species are the smallest produced by any of the species of *Corallobothrium* thus far described.

Because of the tremendous difference in the length as compared with the other two species, the smaller number of testes, and the great difference in the egg measurements, besides the other distinct characters to be pointed out, I regard the parasite under consideration as a new species which I shall designate as *Corallobothrium giganteum*. This name was given not only because it is the largest species of its genus but also because it is one of the largest known cestodes infesting fresh-water fish.

	Max. length	Sucker sphincter	No. of testes	Second egg membrane	Size of oncosphere
<i>C. solidum</i>	4 cm.	absent	140 to 180	20 to 24 $\mu$	13 to 16 $\mu$
<i>C. giganteum</i>	44 cm.	present	80 to 100	14 to 19 $\mu$	8 to 13 $\mu$
<i>C. fimbriatum</i>	8 cm.	absent	100 to 125	28 to 36 $\mu$	16 to 24 $\mu$



Only a superficial examination is necessary to separate this species from *Corallobothrium solidum* or *C. fimbriatum*. Besides the points considered in the preceding comparison, *C. giganteum* is distinct from the other species in the character of the scolex (Figs. 5, 10, and 15), the size and shape of the proglottids, shape of the ovary, and in the less extensive development of the uterus. The measurements in the preceding comparison were made on preserved material.

#### CORALLOBOTHRIUM FIMBRIATUM NOV. SPEC.

This cestode is usually found in the anterior portion of the intestine of *Ictalurus punctatus*, *Leptops olivaris*, or *Ameiurus melas*. The length, when ripe proglottids are present, varies from 15 to 80 mm among preserved specimens. The maximum breadth reaches 2.6 mm. Living individuals frequently reach a length of 70 to 90 mm when well extended. The strobilization is very distinct and the segments are more easily detached than those of *C. giganteum*. The number of proglottids ranges from 40 to 90. They vary in shape and size according to the state of contraction and the body size of the individual. The following measurements in millimeters were taken from 6 prepared specimens:

##### Immature proglottids

length 0.09, 0.16, 0.41, 0.19, 0.53, 0.16, 0.31, 0.27, 0.21

breadth 0.78, 0.46, 2.40, 1.57, 1.89, 1.68, 1.36, 1.15, 0.56

##### Mature proglottids

length 1.00, 0.95, 1.05, 0.50, 0.63, 0.73, 0.73, 0.63

breadth 1.9, 1.26, 1.36, 0.59, 1.26, 1.26, 2.60, 1.05

##### Ripe proglottids

length 1.05, 1.05, 1.01, 1.05, 1.00, 0.94, 1.05, 1.36, 1.36, 0.84

breadth 1.78, 2.60, 1.01, 1.01, 1.20, 1.36, 1.05, 0.73, 0.73, 0.84

The thickness varies from 0.5 to 0.7 mm. The immature and mature proglottids are almost invariably broader than long, while the ripe segments are longer than broad. In transections some ripe proglottids are flattened dorsally but rounded ventrally; in others the reverse is true.

In the descriptions of *C. solidum*, with which this form agrees very closely, that of Fuhrmann (1916) is the only one containing adequate measurements. He records the length of first proglottids as 0.09 mm; 5 mm behind the scolex as 0.23 mm and posterior segments as 0.65 mm. He gives the same maximum length and breadth as did Fritsch (1886) since he used the latter's preparations. Janicki (1926) gives the maximum length as 60 mm and maximum breadth as 3.5 mm but fails to record any other measurements for the proglottids. I have been unable to find in any *C. fimbriatum* specimens the definite surface structure which Janicki describes and figures for *C. solidum*. He states, "Von den zwei

mir vorliegenden Exemplaren weist das grössere eine sehr eigentümliche Gestaltung der Körperoberfläche auf, indem die Rindenschicht durch tiefe longitudinal wie transversal verlaufende Einkerbungen das Bild einer mosaikartigen Täfelung hervorruft." There are, to be sure, longitudinal and transverse grooves which are largely the result of contraction (Fig. 1), but they are never as regular in occurrence as Janicki indicates for *C. solidum*.

This species possesses the same type of scolex as *C. solidum* and *Goezeella siluri* Fuhrmann 1916. It measures from 1.26 to 3.75 mm in transverse diameter. The latter measurement was found in only one case and then the scolex was completely expanded. Figure 4 represents the scolex in a more expanded condition. Among 15 individuals bearing ripe proglottids the scolex usually measured about 2 mm in transverse diameter. The dorso-ventral is always less than the transverse diameter. In one fully expanded scolex the former is 2.31 mm and the latter is 2.61 mm. It is evident that the scolex of this species is subject to such extremes that many individuals must be studied to establish the range in size. When fully expanded, the scolex appears as a disc surmounting the proglottids and is set off sharply from the neck. In some contracted specimens the scolex is not thus sharply set off (Fig 1). The collar-like structure which surrounds the suckers may be folded over them laterally and dorso-ventrally, thus concealing them from view. Extending from each of the suckers toward the periphery of the scolex are deep grooves which mark the limits of the folds just described. The anterior surface of the scolex thus frequently resembles that of *Ephedrocephalus lobosus* as figured by Riggenbach (1896, Pl. 8, fig. 23b). The apex may be protruded as shown in figure 22, or it may be invaginated as indicated by figure 19. A rostellum is lacking, and hooks of any kind are absent.

Four suckers are situated in the anterior surface of the scolex. Their form and size vary according to the state of contraction. The following measurements in millimeters were made on sectional material:

Length 0.36, 0.43, 0.41, 0.37, 0.37, 0.38, 0.33, 0.45, 0.33, 0.53

Diameter 0.56, 0.53, 0.51, 0.37, 0.41, 0.40, 0.41, 0.38, 0.43, 0.60

Diameter of opening 0.13, 0.19, 0.21, 0.06, 0.06, 0.06, 0.12, 0.18, 0.18, 0.23

The measurements which follow were taken from toto-mounts:

Length 0.30, 0.23, 0.23, 0.19, 0.26, 0.39, 0.51

Diameter 0.38, 0.26, 0.26, 0.23, 0.23, 0.53, 0.88

Diameter of opening 0.16, 0.09, 0.06, 0.11, 0.13, 0.13, 0.41

A description of the musculature of the scolex and its suckers is unnecessary, since there is no apparent difference in this regard between *C. fimbriatum* and *E. lobosus* as described by Riggenbach. The peculiar,



knob-like structure or sphincter found in the suckers of *C. giganteum* is wanting here. In the three descriptions of *C. solidum* the size of the suckers is not given. From Fritsch's figure which was drawn to scale, I estimated the length of the suckers as 0.6 mm and the width as the same.

A neck is present, but its dimensions are dependent upon the state of contraction and the size of the specimen. Among eight individuals the neck in three was longer than wide, but in five cases it was wider than long. In millimeters the necks measure as follows:

Length 0.46, 0.63, 0.46, 0.53, 0.72, 0.96, 1.05, 1.26

Breadth 0.33, 1.89, 0.36, 0.56, 0.86, 1.21, 1.57, 0.94

In his description of *C. solidum* Fritsch states, "Man erkennt ohne Schwierigkeit, dass die schmalen, ohne Vermittelung eines Halses dem Kopf angefügten Glieder, sehr bald geschlechtsreif werden." Fuhrmann, using the same preparations, reports a short neck, while Janicki states that no neck is present in the specimens examined by him.

The cuticula of this species varies from 5 to 9 $\mu$  in thickness which corresponds very closely to that of *Corallobothrium giganteum*. It is divided into two layers, an inner which stains deeply with hematoxylin, and an outer layer which stains very little. Beneath the cuticula courses the very thin basement membrane (less than 1 $\mu$ ). The subcuticular musculature shows a variation from the usual condition since the longitudinal fibers, which are present in a single layer, lie closely applied to the basement membrane. The usual layer of circular fibers was not distinguishable. Beneath the muscle fibers just described occur the spindle-shaped subcuticular cells which constitute a layer about 0.03 mm thick. The cortical parenchyma is very loosely constructed. In some sections it reveals a network of rounded spaces which measure from 6 to 35 $\mu$ .

The musculature of this form is highly developed, but less so than in *C. giganteum*. Separating the cortical and medullary parenchyma are found the inner longitudinal muscles which constitute a layer from 16 to 30 $\mu$  thick. These fibers are arranged in irregularly shaped bundles, but the bundles are not grouped in layers (Fig. 27). In *C. solidum* both Fuhrmann and Janicki report that laterally the muscles are more highly developed. This is also the case in *C. fimbriatum*. In this species transverse bundles, within the longitudinal muscle layer, are very numerous in immature proglottids; but in mature segments they are crowded against the longitudinal bundles by the growth of the reproductive organs. Many dorso-ventral bundles are present between the pouches of the uterus and in the lateral margins of the medullary parenchyma.

The nervous system consists of a nerve ring situated in the apex of the scolex near the anterior level of the suckers. A nerve trunk which measures 0.03 mm in diameter arises from each side of the ganglion and

passes posteriad between the outer margins of the two pairs of suckers. These trunks extend throughout the strobila in the lateral margin of the medullary parenchyma close to the longitudinal muscle sheath, as in *C. giganteum* and most Proteocephalids.

The excretory system is highly developed, but less so than in *C. giganteum*. It represents the typical condition as there are two pairs of vessels, a dorsal or ascending pair, and a ventral or descending pair. The former are more lateral in position and are found throughout the strobila closely applied to the nerve trunks. Their course is much less tortuous than that of the descending vessels. No branches could be found issuing from them. In ripe proglottids they measure about  $4\mu$  in diameter, but proceeding anteriorly the diameter increases until in the neck region it may attain as much as  $24\mu$ . The structure of the wall of the ascending trunk is very similar to that described for *C. giganteum* (Fig. 40). Frequently in ripe proglottids the vitellaria surround the dorsal vessel and it might be mistaken for a longitudinal vitelline duct.

The descending trunks, as already mentioned, describe a tortuous course. Their position is less rigidly fixed than that of the ascending vessels, because of the crowding of the reproductive organs, but they are always found in the ventral medullary parenchyma proximal to the ascending vessels. Their diameter varies from  $24$  to  $40\mu$ . Their walls are much thinner than those of the ascending vessels. The cross commissure which connects the descending vessels and the small vessels leading to the exterior which have been described for *C. giganteum*, are wanting in *C. fimbriatum*. Likewise I have been unable to discover any such vessels as Janicki has described for *C. solidum*. He states: "Die Foramina secundaria gelangen im hinteren Teil der Proglottis auf der ventralen Seite zur Entwicklung und stehen vermittelt besonderer Zweiggefäßen mit den zwischen den grossen Ventralstämmen sich ausspannenden und vielfach secundär aufgelösten Commissuren in Verbindung." At no point can I find any vessels passing beyond the inner longitudinal muscle sheath. The behavior of the ascending and descending vessels in the scolex is almost identical with that already described for *C. giganteum*.

#### *Reproductive Organs*

The common genital sinus occurs irregularly alternate on the lateral margin of the proglottid, almost invariably within the anterior fourth of the segment. A genital papilla is lacking in this species. The character and arrangement of the reproductive organs is typically Proteocephalid, as all the sex organs are contained within the inner longitudinal muscle sheath.

In immature proglottids where the testes are not crowded upon themselves or upon other organs, they are typically spherical and measure from 0.02 to 0.04 mm in diameter. In the mature proglottids, their shape varies from spherical to elongate oval, the form being dependent on the degree of pressure to which they are subjected (Fig. 32). The spherical testes measure from 60 to 72 $\mu$  in diameter while the others range from 64 $\mu$  long by 48 $\mu$  wide to 80 $\mu$  long by 72 $\mu$  wide. The number of testes present in mature proglottids ranges from 100 to 125. Before the uterus has undergone a great deal of development the testes occupy all the available space in the medullary parenchyma (Fig. 14), but as the uterus grows it crowds the testes dorsally and laterally (Fig. 31). In mature proglottids only a single layer is present dorsal to the uterus, and only two or three layers are usually found lateral to it. In ripe proglottids the testes are crowded out of the lateral portions of the medullary parenchyma by the uterus, which extends to the vitellaria on each side (Fig. 31). They are found between the uterine pouches and frequently in the ventral portion of the medullary parenchyma. In the fully ripe segments they have almost completely disappeared.

Vasa efferentia were not distinguishable in any of the preparations. The vas deferens which measures from 16 to 50 $\mu$  in diameter is extremely well developed. Its coils, from 25 to 30 in number, extend from the mid-line of the segment to the cirrus-pouch (Fig. 14). In immature segments they occupy nearly the anterior fourth of the medullary parenchyma, but when the segments become mature they are forced dorsally or between the pouches of the uterus (Fig. 29). Spermatozoa are present in the vas deferens when the uterus is in a very early stage of development (Fig. 14), i.e., in proglottids which are otherwise immature. Upon reaching the cirrus-pouch the vas deferens passes over into the ductus ejaculatorius. In immature segments it proceeds to the cirrus without coiling but in mature and ripe proglottids it describes three or four coils before emptying into the cirrus. Its diameter, upon entering the cirrus-pouch is about 16 $\mu$ , but it widens as it proceeds, and frequently it may reach a diameter of 30 to 40 $\mu$  before emptying into the cirrus. As it enters the cirrus it narrows again to about 16 $\mu$  in diameter.

When inverted, the cirrus measures from 0.13 mm long by 25 $\mu$  wide to 0.19 mm long by 36 $\mu$  wide. It is typically club-shaped, with the narrow end at the proximal portion of the cirrus-pouch. When everted the cirrus measures from 0.16 to 0.23 mm in length and from 40 to 44 $\mu$  in greatest diameter. It tapers gradually from its proximal to its distal end, where it measures about 0.02 mm in diameter. A terminal dilatation is wanting (Fig. 36). The cirrus-pouch varies from elongate oval, when the cirrus is inverted, to gourd-shape, when the cirrus is everted. It measures from 0.17 to 0.24 mm in length and from 0.07 to 0.09 mm in greatest



diameter. None of the descriptions of *C. solidum* record the size of the cirrus inverted or everted. The cirrus-pouch according to Fuhrmann is pear-shaped and measures 0.5 mm long by 0.22 mm wide. Janicki makes no reference to the shape but reports the length as 0.34 mm. The structural details of the vas deferens, cirrus and cirrus-pouch do not vary from those described for *C. giganteum*.

As in *C. giganteum*, the vagina opens into the genital sinus beside the cirrus in a horizontal plane, and may be either anterior or posterior to the latter. Both the cirrus and vagina pass into the medullary parenchyma between the dorsal and ventral excretory vessels and ventral to the longitudinal nerve trunk.

From the genital sinus the vagina passes along the ventral margin of the medullary parenchyma for about one-fourth of the proglottids diameter; then it courses dorsally and posteriorly to the mid-line of the proglottid, which it follows to the level of the ovarian commissure (Fig. 29). The course of the lower vagina will be discussed presently.

A sphincter vaginae is absent, or only weakly developed. The first part of the vagina, or the portion that usually extends from the genital sinus to about the mid-line of the segment, measures from 11 to 16 $\mu$  in diameter. Its walls are somewhat heavier than those of the succeeding portion. The second portion of the vagina is thin-walled, and frequently reaches 32 $\mu$  in diameter, but in such cases it is distended with spermatozoa. This portion of the vagina functions as a receptacle for spermatozoa. A distinct seminal receptacle, such as is found in *C. giganteum* is not present. Fuhrmann states that a seminal receptacle is wanting in *C. solidum*. Near the level of the ovarian commissure the second portion of the vagina is greatly reduced in diameter, giving rise to the narrow, more muscular, lower vagina which measures from 8 to 12 $\mu$  in diameter. It passes dorsal to the ovarian commissure and follows along the lateral margin of the shell gland. Near the posterior margin of the segment it empties into the oviduct (Fig. 41).

The bi-lobed ovary lies in the posterior portion of the proglottids midway between the dorsal and ventral longitudinal muscles. In some transections the ovary presses against the dorsal and ventral longitudinal muscles thus filling much of the medullary space in the posterior end of the segment. Its shape may be roughly omegoid (Fig. 9) or it may be pyramidal (Fig. 8). The contraction of the segment affects the shape very materially. When much contracted, each wing of the ovary shows several secondary lobes (Fig. 12), which are less evident when the segment is fully extended (Fig. 13). A commissure joins the inner anterior margins of the two wings of the ovary. The inner posterior margins pass around the shell gland and proceed toward the median line but do not join. From the shell gland the two wings extend laterally. The pos-

terior margin of each wing parallels the septum of the segment, but the anterior margin dips down gradually until near the vitellaria on each side the two margins meet in a rather acute angle. Figures 8, 9, 12 and 13 represent some of the variations in the shape of the ovary. In an expanded ripe segment 1.58 mm wide the ovary measures 0.79 mm in diameter and only  $66\mu$  at the point of greatest length. In an expanded mature segment 1 mm wide the ovary measures 0.56 mm wide and 0.01 mm through the region of greatest length.

The following measurements in millimeters were made on mature segments which were more or less contracted:

Width of segment: 1.15, 1.11, 1.19, 1.26, 1.26

Width of ovary: 0.45, 0.46, 0.53, 0.54, 0.53

Length of ovary: 0.22, 0.23, 0.24, 0.21, 0.23

These measurements indicate that the width of the ovary is a little less than half the proglottid diameter.

Near the median line, and on the ventral surface, the commissure empties into the oocapt which measures from 28 to  $38\mu$  in diameter and is surrounded by a layer of gland cells about  $16\mu$  thick (Fig. 29). Fuhrmann gives the diameter of the oocapt of *C. solidum* as  $28\mu$ . From the oocapt the oviduct, whose maximum diameter is about  $24\mu$ , proceeds along the lateral margin of the interovarian space. Just before reaching the intersegmental septum it changes direction and crosses the interovarian space. Near the opposite side it bends posteriad and dorsad. After receiving the lower vagina it passes along the posterior margin of the proglottid. Upon reaching the middle of the interovarian space it turns anteriorly. Near this point it receives the vitelline duct and empties immediately into the ootype (Fig. 41).

The ootype, which measures from 12 to  $16\mu$  in diameter, lies in the dorsal portion of the medullary parenchyma. It is surrounded by the shell gland which is highly developed and measures from 0.09 to 0.16 mm. in diameter (Fig. 32). From its connection with the oviduct the ootype continues anteriorly from 0.09 to 0.10 mm, then it empties into the uterine passage. The uterine passage is a very thin-walled tube measuring from 16 to  $20\mu$  in diameter. From the ootype it proceeds anteriorly and dorsally. After making several coils it empties into the uterus near the middle of the proglottid.

The uterus begins growth in the ventral region of the medullary parenchyma but as it develops takes up more and more space, until in the ripe proglottids it crowds the vitellaria, excretory vessels and longitudinal nerves at each side, and occupies all possible space (Figs. 25, 31). The testes, vas deferens and other organs are crowded between the uterine pouches or flattened against the longitudinal muscle layer. The ovary is frequently pressed against the posterior limit of the segment



to such an extent that it is distorted in shape and may be difficult to distinguish (Fig. 25). At this stage the proglottid is hardly more than an egg-sac. From the main uterine stem arise from 10 to 14 uterine pouches, each of which in turn produces from 2 to 5 secondary pouches (Figs. 29, 32). On the ventral surface of the ripe proglottids occur one or two uterine pores.

The vitellaria form two lateral columns which extend from the anterior to the posterior region of the segment. They are more dorsal than ventral in position. The ventral excretory vessels lie beneath them. Their transverse diameter, which is dependent on the amount of contraction, ranges from 0.06 to 0.19 mm. At the level of the ovary or near the posterior limit of the proglottid each column turns inward until it comes in contact with the wings of the ovary (Fig. 14). From these inward-directed portions arise two vitelline ducts, one from each side, which run ventrad and meet lateral to the oocapt, forming the common vitelline duct, this proceeds dorsally and empties into the oviduct near its union with the ootype. The diameter of the two ducts just mentioned depends on the presence of vitelline cells; when empty they are indistinguishable, but when they contain vitelline cells the lumen measures from 11 to 16 $\mu$ . At the point where the lateral ducts empty into the common vitelline duct a diameter of 32 $\mu$  is frequently attained. From this region to its union with the oviduct the common vitelline duct measures only from 16 to 24 $\mu$  in diameter. A distinct vitelline reservoir, like that in *C. giganteum*, is lacking in this species (Fig. 41). The vitelline cells present in the ducts are ovoid in form and measure from 11 to 14 $\mu$  through their long axes.

This species shows amphitypy, the same irregularity in the arrangement of the organs of the interovarian space as described for *C. giganteum*; that is, in successive segments a complete reversal occurs. This reversal is not correlated with the right or left position of the genital pore, nor with the position of the vagina with reference to the cirrus. The organs may be arranged as shown in figure 41 or they may be just the reverse. In five successive segments the arrangement of the organs as shown below was observed.

Genital Pore	Left	Left	Left	Right	Right
Vagina anterior		+	+		+
Vagina posterior	+			+	
Oviduct right			+	+	
Oviduct left	+	+			+
Vitelline duct right	+	+			+
Vitelline duct left			+	+	
Lower vagina right			+	+	
Lower vagina left	+	+			+

A description of the living egg of the species is given later. Only the interuterine eggs of prepared specimens will be considered here. The outer membrane, which is so prominent just after the eggs have been discharged into the water (Fig. 42), is very difficult to see in sectional material. The second membrane is clear and since it is rather heavy its size is not affected greatly by preservatives. Its form is not spherical but is somewhat longer than broad. Through the long axis it measures from 28 to 36 $\mu$ , the average being about 34 $\mu$ . The contained oncosphere measures from 16 to 24 $\mu$  in diameter, the average being about 20 $\mu$ .

The eggs of this species are larger than those of *C. giganteum*. Fuhrmann reports the eggs of *C. solidum* as being small; "die Oncosphaere hat einen Durchmesser von 0.013 to 0.016 mm, die äussere Schale einen solchen von 0.020 to 0.024 mm" Janicki remarks: "Die reifen Eier von *C. solidum* sind ausserordentlich klein, sie messen nur 0.020 mm im Durchmesser, erscheinen aber sehr charakteristisch, so dass sie nicht leicht mit Eiern eines anderen Cestoden verwechselt werden können."

The foregoing description indicates that *C. fimbriatum* bears a close resemblance to *C. solidum*, but the following comparison shows some very outstanding differences between the two forms.

	Foramina secundaria	No. testes	Size of second egg membrane	Size of oncosphere
<i>C. solidum</i>	Present	140 to 180	20 to 24 $\mu$	13 to 16 $\mu$
<i>C. fimbriatum</i>	Absent	100 to 125	28 to 36 $\mu$	16 to 24 $\mu$

A lack of specific information on a great many points in the descriptions of *C. solidum* prevents a more complete comparison. The above data, however, are sufficient to mark the cestode under consideration as distinct from *C. solidum*. It is therefore regarded as a new species, which is designated as *Corallobothrium fimbriatum* because of the fringed character of the scolex.

## DISTRIBUTION, ABUNDANCE AND SEASONAL OCCURRENCE

*Corallobothrium giganteum* and *C. fimbriatum* have been found associated in the intestinal tract of *Ictalurus punctatus*, *Ameiurus melas* and *Leptops olivaris* taken from the Rock, Mississippi and Illinois rivers. An intensive study was made only of *I. punctatus* from the Rock River, 130 of that species being examined during 1926. Nearly 70 per cent showed infection with one or both species of *Corallobothrium*. The following table is confined to the data on the adult parasites.

TABLE I  
OCCURRENCE OF ADULT CORALLOBOTHRIUM

Date	Host	Number Examined	Stream	Number <i>C. fimbriatum</i>		Number <i>C. giganteum</i>	
				Present	Average	Present	Average
October, 1924	<i>A. melas</i>	3	Rock River	0	0	0	0
" "	<i>I. punctatus</i>	5	" "	0	0	0	0
June, 1925	<i>I. punctatus</i>	8	" "	16	2	21	2.6
" "	<i>I. punctatus</i>	1	Mississippi R.	10	10	8	8
July, 1925	<i>L. olivaris</i>	1	" "	1	1	1	1
December, 1926	<i>A. melas</i>	2	Illinois River	0	0	0	0
November, 1927	<i>A. melas</i>	5	" "	0	0	0	0
April, 1926	<i>I. punctatus</i>	14	Rock River	0	0	0	0
June, "	" "	10	" "	25	2.5	15	1.5
July, "	" "	46	" "	42	0.95	61	1.3
August, "	" "	25	" "	12	0.48	6	0.24
September, "	" "	6	" "	0	0	4	0.66
November, "	" "	11	" "	0	0	0	0
December, "	" "	18	" "	0	0	0	0

It is evident from the preceeding data that the adult form of *Corallobothrium* appears in the late spring or early summer, reaches its maximum during June and July, and disappears entirely the latter part of October or the first part of November. Additional data on the seasonal occurrence of *Corallobothrium giganteum* and *C. fimbriatum* have been secured by an examination of the parasites collected by Mr. R. E. Richardson of the Illinois Natural History Survey, in connection with his studies on the food of *Ictalurus punctatus*. Only the stomach and about 5 cm of the intestine of each fish were preserved for his investigation. From such a limited portion of the intestinal tract, at best, only a small per

cent of the parasites present in each fish could be secured. In all, 1252 individuals were examined. From 954 *I. punctatus*, which were collected from June to September, 35 showed the presence of either one or both species of *Corallobothrium*. Among 278 of the same species of fish, collected from October to May, no parasites were recorded. While to be sure, a much larger number was examined during the period from June to September nevertheless a sufficient number was studied throughout the months from October to May to warrant the expectation of a proportionate percentage of parasitized fish, had the cestodes been present to the same degree during the whole year. Taken independently, these data would not be significant, but in connection with the evidence shown in Table 1 there can remain little doubt that the adult form of both species of *Corallobothrium* occurs only from spring to fall in *I. punctatus*.

Meggitt (1914) in his study of *Proteocephalus filicollis* states: "Almost every fish in autumn was infected with one or more of these parasites, 75 per cent of which were adult; in winter, the number of infected fish was considerably smaller, and adults were rare; while in spring, the proportion of adults again increased." He goes on to say that von Linstow failed to find adult *P. filicollis* at all in winter, and Zschokke noticed it only three times. Wagner (1917) makes the following statement regarding *P. torulosus*: "Wie verschiedene Autoren (Zschokke, v. Linstow, Kraemer, Riggensbach) übereinstimmend berichten, fällt die Reife der Geschlechtsprodukte der Fishtänien in Zeit zwischen Frühling und Herbst. Im Winter sind immer nur junge, noch nicht geschlechtsreife Tiere gefunden worden, was auch meine Erfahrungen an *I. torulosa* bestätigen." Thus my findings for *Corallobothrium* agree, for the most part, with those of *Proteocephalus filicollis* and *P. torulosus* as just quoted.



## LIFE HISTORY OF CORALLOBOTHRUM

Gruber, (1878) in his study of the copepods of Lake Constance, was the first to discover a larval cestode in the body cavity of a Cyclops. He found and described a proceroid from *C. brevicaudatus* and made the following conjecture: "Die Entwicklung zur Taenia erfährt der Wurm ohne Zweifel im Darne eines der zahlreichen Fische welche sich von den kleiner Krustern des Sees ernähren und es möchte wohl am wahrscheinlichsten sein, der Jungendzustand der *T. torulosa* ist, welche nach Rudolphi und Dujardin in Cyprinoiden unser Süßwasserseen lebt, obgleich es mir bis jetzt noch nicht gelungen ist, dieselbe aufzufinden." Following Gruber's discovery papers appeared by Mrazek, v. Linstow, and others, which described proceroids from Cyclops, Diaptomus, Gammarus and various ostracods. In many instances the larvae were identified with known adult parasites, but such studies usually admit of considerable doubt. Schmidt (1894) was the first to feed tapeworm eggs experimentally to the smaller aquatic crustacea. He succeeded in infecting *Cypris ovata* with the eggs of the duck tapeworm, *Taenia anatina*, and described the development of the latter species from the oncosphere to the mature proceroid (Cysticerkoide).

Linton (1891) published a contribution to the life-history of *Dibothrium cordiceps* in which he says, "I have found a large Dibothrium in the white pelican (*Pelecanus erythrorhynchus*) which is evidently the adult form of *D. cordiceps*, of which the trout (*Salmo mykiss*) is the intermediate host." Linton gives no experimental evidence to substantiate his supposition. Consequently his conclusions are largely conjectural. No experimental work was done on the first intermediate hosts of fish cestodes until the work of Schneider (1903) who infected *Gammarus locusta* with the eggs of a species of *Proteocephalus*, Barbieri (1909) described a new cestode from *Alsosa finta* var. *lacustris* which he called *Ichthyotaenia agonis*. On insufficient evidence he gives the intermediate hosts for his cestode as Bythotrephes and Leptodora.

A successful study of the complete life-cycle of a fish cestode was made by Meggitt (1914), who traced the complete development of *Proteocephalus filicollis* by experimental methods. *Cyclops varius* was found to be the first and only intermediate host. *P. filicollis* is parasitic in the stickleback. The latter is infected by ingesting Cyclops which contain mature proceroids of *P. filicollis*.

Wagner (1917) made a splendid experimental study of the developmental cycle of *Proteocephalus torulosus*, for which he discovered *Cyclops strenuus* and *Diaptomus castor* as the first intermediate hosts. The fish



host, *Cyprinus orfus*, is infected with *P. torulosus* by feeding on copepods, some of which are infected.

Janicki and Rosen (1917) published the results of their successful study on the manner in which fish were infected with the plerocercoid of *Diphyllbothrium latum*.

Following this work, Rosen (1918) elucidated the life-history of two other species, viz., *Triaenophorus nodulosus* and *Abothrium infundibuliforme*. A year later the same worker outlined the development of *Ligula simplicissima*. It was found that the life-cycles of these forms were almost identical, excepting in *A. infundibuliforme*, the mature egg gives rise to a ciliated larva; the egg of that species, however, produces in the water an unciliated larva. In each case these larvae are eaten by some species of Cyclops and the subsequent development is practically the same. All of these cestodes except *A. infundibuliforme* require a second intermediate host, which is found among the young fish inhabiting the same waters. The adult host of *D. latum* is man, the dog, or possibly the cat; that of *T. nodulosus* and *A. infundibuliforme* is found among the fish, while that of *L. simplicissima* is some species of aquatic bird.

The literature contains no further studies on the life cycles of fish cestodes until the appearance of a fine paper by Kuczkowski (1925). This worker succeeded in infecting *Cyclops strenuus*, *C. serrulatus* and *C. oithonoides* experimentally with the eggs of *Proteocephalus percae* which is parasitic in *Gasterosteus aculeatus*, and likewise *C. strenuus* and *C. serrulatus* with the eggs of *P. longicollis* which is parasitic in *Coregonus albula*. In this study, Kuczkowski, gave particular attention to the development of the bladder appendage, or "cercomer," and its bearing on the "cercomer theory." Bangham (1925), in his studies of the cestode parasites of the black bass, reports that the proceroids of *P. pearsei* were found in a species of Cyclops and also in *Epischura lacustris*. Since no experimental work was done to establish the identity of the larvae there remains considerable doubt whether they were the proceroids of *P. pearsei* or some other Proteocephalid.

The papers just mentioned represent the work that has been done on the life-cycles of fish cestodes in Europe and America up to the present time. Therefore the study of the developmental history of fish cestodes from American hosts offers a nearly unexplored field. The investigation reported here was undertaken in the hope that some definite information might be obtained on the developmental cycle of the two species of American fish cestodes just described.

#### OBSERVATIONS CONCERNING THE EGGS

After the cestodes were removed from the intestine of the fish, they were washed immediately in tap water. This was done by grasping the

worm near the middle with a pair of forceps and rapidly raising and lowering it in the water. Each adult individual was then placed in a separate watchglass and covered with cold water. The excessive contractions of the worms caused the eggs to be ejected in milk-colored streams from the uterine pores of all the ripe proglottids. It was estimated that upward of a million eggs were emitted by an average-sized adult *Corallobothrium giganteum*, and one-half million or more by an adult *C. fimbriatum*. According to LaRue (1914) the eggs of the Proteocephalids usually have three membranes. The outermost membrane is thin, hyaline and spheroidal in form. The middle membrane is thick and granular. The innermost membrane is a clear, delicate but tough structure which is closely applied to the embryo.

The eggs of *Corallobothrium fimbriatum* are typically spherical, usually flattened and depressed at each pore. In their general outline they recall the form of an apple. The diameter varies from 0.08 to 0.14 mm. The outer membrane encloses a thick layer of transparent, gelatinous substance which is responsible for the unusually large size of these eggs (Fig. 42). At the center of the gelatinous material is found a second membrane which is ovoidal in form, varying in size from 36 to 38 $\mu$  by 30 to 32 $\mu$ . The structure of this membrane is homogeneous and firm. It does not have a granular appearance in the living material nor in the eggs sectioned in the uterus. It presents rather the character of a chitinous covering which closely resembles, and is doubtless homologous to, the shell of the Bothriocephalan egg. Meggitt (1914) reports an aperture in the second membrane of the eggs of *P. filicollis*. I have not observed such an opening in the eggs of either species of *Corallobothrium*. Lying beneath the second membrane of the eggs of *Corallobothrium fimbriatum* is a dense layer of granular substance about 0.10 mm thick. This material is doubtless composed of vitelline granules and other substances, either stored for the nourishment of the oncosphere or cast off during its formation. Surrounded by the granular layer just mentioned is found the six-hooked embryo. A third membrane could not be distinguished in either living or sectional material. The membranes of the living egg are so transparent that the oncosphere, which is about 20 $\mu$  in diameter, can be seen distinctly. By a series of gliding movements it turns itself about within the shell or second membrane. Coincident with the movements of the body, the hooks are repeatedly extended and withdrawn. Observations made successively on the same individual for 12 hours showed that the oncosphere continued its apparent efforts to escape from its enclosing membranes. Its movements were rather spasmodic and intermittent. A period of vigorous contortions, during which it would frequently turn itself completely about, would be followed by a longer period of inactivity. On several occasions oncospheres were observed to work their way through

the granular layer and reach the shell, against which they repeatedly brought their hooks with all possible force but without apparent effect. The second membrane or shell seemed impervious to the action of the hooks. These observations indicated clearly that the oncospheres could not escape from the egg membranes by their own efforts.

Frequently in studying the eggs the rupture of the shell was noted. This permitted the escape of the oncosphere into the gelatinous covering (Figs. 43, 46). I could not always attribute the ruptured shell to the pressure of the coverglass. Meggitt (1914) who observed the same phenomenon in the eggs of *P. filicollis* offers the following explanation: "The cause of its [the oncosphere's] escape may be possibly due to osmosis, but it is more probable that it is due to the oncospheric movements." That is, the oncosphere forces its way out of the shell through the aperture which has already been mentioned. My observations on the structure of the shell and the activity of the oncosphere of *Corallobothrium fimbriatum* make the latter explanation untenable. When the oncosphere is found free in the gelatinous covering its structure and movements are more easily observed. The body of the oncosphere is covered by a very delicate membrane in which the proximal ends of the hooks are embedded. Within this membrane is the plasma, a grayish mass of homogeneous substance containing extremely fine granules. The plasma vividly recalls the color and structure of the protoplasm found in *Amoeba proteus*. Cell boundaries could not be distinguished, and it was quite impossible to detect the presence of any structures that might be interpreted as muscle fibers.

To determine the method by which the hooks of the oncosphere were brought into action, a long series of observations was necessary. The hooks are arranged in three pairs near the periphery of one pole of the embryo. Two pairs are placed laterally, while the third pair lies between. Usually the proximal ends of the hooks lie close together while the distal ends, bearing the hooks proper, are more widely separated. Before being thrust out the lateral pairs are brought up close to the middle pair. When this movement is completed the hooks of each pair are parallel with each other (Fig. 46). After watching their movements for hours, it became quite evident that the hooks were incapable of independent action; that their extension only occurred when the body of the oncosphere was elongated (Fig. 43); and that their return to a position of rest occurred only when the oncosphere again assumed a spherical form, i.e., the elongation of the oncosphere extended the hooks and its contraction withdrew them. The presence of muscle fibers attached to the hooks is extremely doubtful. My observations lead me to the conclusion reached by Janicki and Rosen (1917) in their study of *Diphyllbothrium latum*, viz., that the hooks, embedded in the membranous covering of the oncosphere, are brought into action as a result of the movements of the plasma rather than through the agency of muscle fibers.



In *Corallobothrium giganteum* only a glance at the eggs is needed to distinguish them from those of *C. fimbriatum* (Figs. 42, 50). The differences in shape and size are noticed at once. They are much smaller, measuring only from 30 to 60 $\mu$  in diameter. Their shape is extremely irregular and varied. These differences are due largely to the distribution of the gelatinous material which surrounds the shell. It usually covers the shell in varying degrees of thickness, with here and there a finger-like projection which may give the egg a star shape. In some instances these projections are absent or less pronounced (Figs. 49, 50). The thickness of the gelatinous material is then more uniform (Fig. 49). The shell itself is almost a perfect sphere, measuring from 21 to 24 $\mu$  in diameter, which is considerably smaller than that of *C. fimbriatum*. A layer of finely granular material is present within the shell, but its thickness is much less than in *C. fimbriatum*. The oncosphere, which ranges from 13 to 16 $\mu$  in diameter, is not surrounded by a third membrane.

Although the structure of the eggs of the two species of *Corallobothrium* is identical, there is wide variation in the amount of the differentiated parts. Thus the ova of *C. giganteum* have less of the outer gelatinous substance, less of the granular material within the shell, and a much smaller oncosphere. Also, the shape and size of the egg as a whole, and the shape and size of the shell are quite different in the two species.

#### *Experiments with the Eggs*

To determine whether or not the eggs would hatch, watchglasses containing several thousand eggs were placed in the dark at room temperature. As a control another watchglass containing a like number of eggs was placed in the light at room temperature. Neither batch of eggs hatched. This experiment, together with observations on the structure of the eggs of each species, indicated that they did not give rise to free larvae but must be ingested in toto by the first host.

It was difficult to determine the viability of the eggs because of the action of bacteria. Thirty-six to forty-eight hours after the isolation of the ova myriads of bacteria began their destructive action upon them but feeding experiments with eggs which had been isolated for four days showed positive results. Eggs liberated in nature would very probably remain viable for a much longer period, since the bacteria should be less numerous in the open waters than under the restricted conditions in the watchglasses. In a medium containing a minimum number of bacteria it is probable that the ova remain viable for eight or ten days, and possibly for a longer period.

To ascertain the manner in which the eggs were disseminated—whether discharged from the proglottid before or after leaving the host—a series of observations were made on live fish. Adult *Ictalurus punctatus* were

placed in the laboratory aquaria, and for three or four successive days after their arrival the feces were examined once or twice a day. The feces were obtained by placing the fish on its back and firmly stroking the abdomen in the direction of the anus. The feces forced out in this way were inspected for the presence of cestode proglottids, eggs, etc. In such examinations of adult fish, eggs were present, but no detached proglottids were found. Furthermore, in post mortem examinations of over 100 adult *I. punctatus*, not a single detached ripe proglottid was recorded. From this evidence and that gained from the study of the adult worm (uterine pore, firmly attached proglottids, etc.), it is concluded that the eggs are forced through the uterine pores and pass out with the feces into the water, where they float about for a time and then sink to the bottom.

#### THE FIRST INTERMEDIATE HOST

In attacking the problem of the life-cycle of these parasites, two methods of approach were considered. First, it seemed reasonable to suppose that some clue to the intermediate hosts of the parasites might be gained by a thorough examination of the stomach and intestinal contents of the fish. Since the larvae of the cestodes probably must enter their final host passively with its food, a systematic study of the food of the fish was made a part of the routine of examinations. Secondly, the intermediate host might be discovered through direct experiment, i.e., by feeding ripe proglottids or eggs to any invertebrate animals which might possibly serve as the first intermediate host of the parasites.

The diet of 55 *Ictalurus punctatus* examined during the months of June and July consisted almost exclusively of crayfish, *Cambarus propinquus*, larval and adult *Hexagenia bilineata*, other insect larvae, and portions of mollusks and fish. The first two of these forms were considered as possible intermediate hosts, and macroscopical and microscopical examinations were made of the remains of those obtained from the stomachs of the fish, but with negative results. It was thought advisable, however, to attempt an infection by feeding them ripe proglottids or eggs.

Experiments with the crayfish, *Cambarus propinquus*, were carried on from July fifth to fourteenth. Crayfish secured from Rock River were placed in laboratory aquaria. After they had been allowed to fast for two or three days, living adult individuals of *C. giganteum* and *C. fimbriatum* were fed to them. Although they did not show a decided preference for the worms, they did eat them. At intervals varying from a few hours to a week after the worms had been ingested, the crayfish were examined. The intestine was removed, its contents teased out on a slide and inspected for the presence of oncospheres that might be in the lumen or for more advanced stages of the larvae encysted in the intestinal wall. Likewise, all the organs contained in the body-cavity were examined, and also the surrounding musculature. The results were negative.



Experiments with the Mayfly, *Hexagenia bilineata*, were made between July twentieth and August fifteenth. While the work with the crayfish was in progress, experiments were conducted on the larvae of *Hexagenia bilineata*. To obtain uninfected material adults were caught and stripped of their eggs, which were placed in large Petri dishes in the laboratory where they were allowed to stand. The water on them was changed every 24 to 48 hours. Seventeen days incubation produced hundreds of small larvae. Eggs of *C. giganteum* and *C. fimbriatum* were placed in two Petri dishes containing fifteen to twenty of these larvae and water-plant. Observations of the larvae under the binocular showed them swimming about or clinging to the vegetation in the containers. None of them seemed to be attracted to the tapeworm eggs. Subsequent examination of the larvae showed no trace of infection with the cestode larvae.

Experiments with *Cyclops albidus* also were conducted during July; these were coincident with the experiments just described. A supply of *Cyclops albidus* was collected from a lagoon near Rock River. A single individual was placed in each of six watchglasses, along with a spray of water-plant. After three or four days it was decided that they could live under such restricted conditions, as all of them were alive and very active. Then a drop of water containing the eggs of *Corallobothrium giganteum* was added to each of three watchglasses; and to each of the other three, a drop of water containing the eggs of *C. fimbriatum*. My observations of the Cyclops under the binocular convinced me that they were not attracted to the cestode eggs. They would, however, readily devour protozoa which were placed with them. On one occasion fork-tailed cercaria, obtained from a snail of the genus *Physa*, were placed in a watchglass with a *C. albidus*. To my great astonishment the Cyclops pounced upon one after another until fourteen were devoured.\* Since efforts to observe the ingestion of the eggs by this species of Cyclops resulted negatively, and since no oncospheres or larvae were found when all of the individuals were afterward examined, it was concluded that further experiments with this species would be futile. It was evident that such a process of elimination applied to each animal which might be suspected of being an intermediate host of these cestodes, would consume much more time than I had at my disposal. Therefore, a more comprehensive method was conceived and pursued.

Mass infection of plankton was accordingly tried from July twentieth to August second. Not far from the Rockford College campus Rock River is obstructed by a dam. By holding a plankton net in the water that poured over this dam, it was possible in a few minutes to collect samples of a large number of the pelagic forms, as well as some bottom organisms that were

\* This may account for the infrequency with which cercaria are met in plankton samples.

caught in the current and carried over the dam. A large quantity of the material gathered by this means was placed in each of two crystalizing dishes. Water-plant of the genus *Cladophora* taken from the face of the dam was placed in each dish. The bottom of one dish was strewn with the eggs of *Corallobothrium giganteum* and that of the other with the eggs of *C. fimbriatum*. Under these conditions all species were subjected to identical conditions; each was given an equal opportunity to ingest the eggs. It was hoped by an examination of the species contained in these cultures that the primary host of each worm might be discovered. After the cultures had stood for eight days, an examination of the different species present was begun. Since among the Copepoda a number of species had been discovered as the primary hosts of cestodes, representatives of that group were examined first. Each copepod was placed on a slide in a small drop of water, then excess water was drawn off with a fine pointed pipette so that only enough water was left to cover the specimen. This procedure minimized its movements and anchored it to the spot so that it could be examined successfully under the microscope. By this method several hundred copepods were examined.

From the culture in which *C. giganteum* eggs were placed, *Cyclops serrulatus* were found to be infected with from 1 to 6 larvae each, while *C. prasinus* were infected with from 1 to 3 each. From the culture inoculated with *C. fimbriatum* eggs, infected individuals were found among *C. bicuspidatus* and *C. serrulatus*, the former usually showing much heavier infection. No infection was observed among the copepods, *C. albidus*, *C. fuscus*, *C. bicolor*, or *Diaptomus*, nor among the Cladocera examined.

Since these results were accepted as a clear indication of the true first intermediate hosts of *Corallobothrium giganteum* and *C. fimbriatum*, further group infections were discontinued and a series of experiments were carried on with isolated groups of the species that had shown infection under mass conditions.

To determine the species and to prevent the inclusion in the experimental groups of individuals infected in nature each *Cyclops* was examined microscopically. Because of the transparency of the *Cyclops*, a cestode larva, when present, could be detected without great difficulty. The uninfected *C. serrulatus* and *C. prasinus* were placed together, and uninfected *C. bicuspidatus* and *C. serrulatus* were also allowed to occupy the same container.

Experimental infection of *Cyclops* was successfully attempted in August. These copepods were placed in a fingerbowl of tap water to which were added a few sprays of water-plant that had previously been rinsed thoroughly to reduce the protozoa in the fingerbowls as much as possible and likewise to prevent the entrance of uninspected *Cyclops*. On August twentieth at 11:30 A.M. the eggs of *C. fimbriatum* were placed in with

them. Oncospheres were found at 3:45 P.M. of the same day in the body-cavity of the Cyclops examined. Thus in a little more than four hours the oncospheres had migrated from the intestine into the body-cavity.

To determine whether or not the ingestion of the tapeworm eggs was selective or accidental, a study of the feeding habits of the Cyclops was undertaken. A fingerbowl containing *C. bicuspidatus* and *C. serrulatus* and the eggs of *Corallobothrium fimbriatum* was observed under the binocular. It was noted that the Cyclops foraged over the sprays of water-plant in the bottom of the fingerbowl and browsed on the particles of debris adhering to the vegetation and to the bottom. Any of the smaller protozoa which came near were instantly consumed. The outer gelatinous portion of the tapeworm eggs was repeatedly trimmed off and eaten, while the inner membrane (shell) containing the oncosphere was rejected. By continuous observation it was revealed that occasionally the inner portion also was taken in with the rest, which indicated that the eggs were eaten only incidentally, along with other organic material on which the Cyclops fed. This condition is in striking contrast with that of *Diphyllbothrium latum* and related forms in which the eggs give rise to ciliated larvae that successfully simulate protozoa and therefore constitute real objects of prey, attracting the Cyclops by their movements and tempting them to pursuit and capture.

The mass infection experiments had shown that *Cyclops serrulatus* could be infected by feeding the eggs of either species of *Corallobothrium*, but this point was not settled in respect to *Cyclops bicuspidatus* and *C. prasinus*. Therefore the eggs of *Corallobothrium giganteum* were fed to *Cyclops bicuspidatus* and those of *Corallobothrium fimbriatum* to *Cyclops prasinus*. The eggs of *Corallobothrium giganteum* were eaten by *Cyclops bicuspidatus* and the oncospheres migrated to the body-cavity, but no development was observed. The oncospheres, five days after the eggs were fed, measured only  $16\mu$  in diameter, their original size. The number present ranged from 2 to 15. This condition was noted in 15 different individuals examined from 1 to 5 days after feeding. The infection of *C. prasinus* with *Corallobothrium fimbriatum* larvae was light; only 2 individuals out of 10 harbored the larvae. The latter, however, were well developed.

#### *Development of Corallobothrium fimbriatum in Cyclops*

When *Cyclops bicuspidatus* and *C. serrulatus* had been identified as the first intermediate hosts of *Corallobothrium fimbriatum*, a study of the successive developmental stages in these copepods was begun. All observations were made on living material and within the period from August twentieth to September fourth. Beginning from one to four hours after feeding, the progress of development was traced through all of the stages found in these animals. As has already been stated, oncospheres were



first observed in the body-cavity of the Cyclops about four hours after the eggs had been placed in the watchglasses. Immediately following their liberation in the intestine of the Cyclops, the oncospheres increased slightly in diameter. While contained in the egg membranes, they measured from  $16$  to  $20\mu$ , but after liberation they measured from  $18$  to  $23\mu$  in diameter. Those present in the body-cavity about four hours after the eggs were fed measured from  $20$  to  $25\mu$ . Their form, however, constantly changed. They did not remain fixed to the intestinal wall of the host by means of their hooks but kept up almost constant motion. Since the elongation and contraction of the body put the hooks in operation, the action of the oncospheres resulted in the repeated extension and withdrawal of their hooks.

After the oncosphere had gained the body-cavity of the Cyclops, development proceeded very rapidly. Twenty-four hours after the eggs had been fed, four oncospheres were liberated, these measured from  $30$  to  $40\mu$  according to the stage of contraction. Figure 53 shows one as it appeared within the abdomen of the Cyclops, while figures 44 and 45 represent their condition 5 to 10 minutes after being liberated. Clear spherical bodies (cells) surrounded by heavy granules were seen throughout the body mass. When first liberated the oncospheres moved about with a gliding movement. During this time the hooks were kept in almost constant motion. Five or ten minutes after the larvae had been removed from the Cyclops indications of degeneration were seen. Then a transparent membrane was pushed out from the body of the oncosphere (Figs. 44, 45). In the individual represented in figure 45 there was a secondary membrane within the outer one from which the parenchyma had withdrawn. Thus it appears that the larvae at this stage possess two membranes; the outer may be considered cuticular while the inner may represent the basement membrane.

Seventy-two hours after feeding, the larvae ranged from  $25$  to  $70\mu$  in diameter (Figs. 55, 48). They were capable of distinct contractions which could be witnessed while they were still within the host. Upon removal, which was accomplished by tearing the Cyclops open by means of two sharply pointed needles, they appeared as a thin-walled sac containing globular bodies representing the parenchymatous tissue, which resembled an emulsion. Their movements were extremely feeble and continued for only a few minutes, then a spherical form was assumed and degeneration soon followed. The hooks, which were widely separated at one pole of the body at this stage, were incapable of effective action.

Four days after feeding, 12 oncospheres, measuring from  $25\mu$  in diameter to  $135\mu$  in length by  $60\mu$  in width, were removed from the body-cavity of one Cyclops. Figure 54 represents the most highly developed individual. Its sac-like body showed considerable differentiation. A cuticular mem-

brane surrounded the body and beneath it the tissue had a striated appearance, due to the development of the subcuticular musculature. Large cells surrounded by more or less heavy granules were evident. A few small calcareous bodies were to be seen scattered here and there throughout the body mass.

On the fifth day a Cyclops was dissected and 14 larvae were present in the body-cavity. These were from 0.06 to 0.24 mm in length. Except for the increase in size, no marked difference between these and the four-day individuals was noted.

One Cyclops observed on the sixth day had 16 larvae in the body-cavity (Fig. 51). Some of these larvae showed an increase in size over those of the fifth day, since they measured from 0.22 to 0.4 mm in length, according to the state of contraction. Upon being liberated, they moved about more vigorously for several minutes. The narrower end, which bore the hooks, showed more activity than the broader portion. Further differentiation had occurred, as the pole at which the hooks appeared presented a striking contrast to the homogeneous structure of the remainder of the body. It had become extremely transparent. The granules which appeared in the remainder of the body were entirely absent in this portion. At the proximal limit of this transparent region, or about 0.04 mm from the extreme body limit, a slight constriction appeared. In some individuals the hooks were attached to this portion, but in others they occurred just beyond the constriction in the granular region of the body (Fig. 56). In a number of cases some of the hooks were present on both regions (Fig. 57).

After six days no further increase in the length of the larvae took place, but many changes in their structural aspects occurred in quick succession. Thus on the seventh day there were evidences of differentiation at the pole opposite that on which the hooks were found. On the eighth and ninth days the larvae showed three distinct regions marked by two constrictions; one delimited the transparent region, the other occurred about one-third of the body length from the pole opposite that which bore the hooks (Fig. 56). By the tenth day, outlines of the developing suckers could be seen in this portion of the body, which was, therefore, the potential scolex.

Larvae studied on the eleventh day after the Cyclops were fed showed the four suckers well developed and at the anterior extremity a distinct end-organ. The large globular cells of the scolex region had disappeared. In their place a reticulum of minute, rounded cells with an occasional muscle fiber had appeared. The calcareous bodies, 5 or 6 in number, were confined, with a very few exceptions, to the middle portion of the larva. The transparent region, more distinctly separated from the middle portion, formed a bladder-like appendage or cercomer (Fig. 57).



The development on the twelfth and thirteenth days differed from that on the eleventh in the following respects: The scolex, which had been differentiated by the eleventh day, was invaginated; the number of calcareous bodies had increased; and the length, by reason of the invaginated scolex, was somewhat reduced (Fig. 58).

Development in the Cyclops is completed by the fourteenth or fifteenth day after the ingestion of the eggs. The best indication of this is the invagination of the scolex and the loss of the bladder, or posterior appendage. Janicki and Rosen (1917) have given this larva the name of proceroid. After this stage is reached the parasite must enter another host before further development can be attained.

To indicate the extent of infection that may occur in such experiments, it should be stated here that from one culture 50 specimens of *C. bicuspidatus* were removed and 46 contained the larva of *Corallobothrium fimbriatum*.

#### *Development of Corallobothrium giganteum in Cyclops*

The development of this species corresponds closely with that of *Corallobothrium fimbriatum*. The oncospheres were observed in the body-cavity of *Cyclops serrulatus* eight hours after the eggs had been placed in the fingerbowls. Their presence was more difficult to detect because of their smaller size and greater transparency (Fig. 52). The number of larvae present in these species of Cyclops varied from 1 to 8. Therefore the infection was less intense than that found in the previous species where as many as 18 larvae were present.

No further observations on the progress of this species were recorded until the eighth day after the eggs were fed. By that time the larvae had attained a length of from 0.28 to 0.39 mm, which corresponded closely to the size of the larvae of *Corallobothrium fimbriatum* at the end of an equal period of time. However, the differentiation of various body regions had progressed considerably more than was true of the *C. fimbriatum* larvae in the same length of time. The suckers and end-organ were distinct and the bladder, or posterior appendage, was almost completely separated from the middle portion; and a larger number of calcareous bodies were present in this species than occurred in *C. fimbriatum* at a much later period. It was also noted that the globular cells, which were very prominent in *C. fimbriatum*, were much less pronounced in these larvae. Aside from the heavy granules scattered through the body, the structure was more homogeneous than that of the other species (Fig. 70).

On the twelfth day an examination of infected Cyclops revealed that the larvae had already become mature proceroids (Fig. 68). This was at least two days earlier than the same stage was reached by *C. fimbriatum*. The cuticula had increased greatly in thickness. The length of the larvae,

which was somewhat reduced by the invagination of the scolex, ranged from 0.2 to 0.25 mm according to the degree of contraction. As was true in the case of the other species, the bladder or posterior appendage had been shed and in addition a well-developed excretory vesicle had appeared in the posterior portion of the body. This organ, which measured from 5 to 9 $\mu$  in diameter, could be traced anteriorly for about 0.06 mm when it became obscured by the surrounding structures. Efforts to detect smaller vessels, which doubtless emptied into it, failed entirely. The vesicle terminated posteriorly in a duct which emptied at the point where the bladder had been attached. Pulsations which began at the anterior portion and passed to the excretory pore, could be seen to proceed rhythmically along its length. An attempt to discover the vesicle in individuals that still possessed the bladder proved futile. There may be a relation between these two structures, besides one of sequence in development, but any statement further than this would be purely conjectural. Such a vesicle was not observed in *C. fimbriatum*. If present, it was obscured by other structures. It was easily seen in a later stage to be described presently.

Twelve-day larvae possessed a greater number of calcareous bodies, from 15 to 25. These were not restricted as in *C. fimbriatum* almost exclusively to the middle body region but were distributed everywhere along the periphery. More of them, however, were present in the posterior portion than elsewhere. The total number in this species is almost twice that discovered in any of the larvae of *C. fimbriatum* of about the same age (Figs. 58, 68).

The suckers and end-organ of the invaginated scolex could not be distinguished clearly in this species, as they were obscured by the overlying tissues. Following their liberation from the Cyclops, the larvae moved about actively for an hour or more. In one or two instances the scolex was evaginated. Figure 64 (*a* to *l*) represents the successive movements and shapes assumed by the larva before the evagination of the scolex. Figure 66 represents the appearance of one specimen with scolex everted after having been fixed and mounted. Maturity in the Cyclops has been reached by this species when the scolex has become invaginated, when the bladder appendage has been shed, and when the excretory vesicle has appeared.

It is interesting to note the difference in the rate of development found in these two species. Although *Corallobothrium giganteum* begins with a much smaller oncosphere, it develops at a rate sufficient to attain maturity in the Cyclops about two days before that point in development is reached by *C. fimbriatum*. Furthermore, the size of the adults in the two species would indicate that this difference manifests itself throughout the developmental cycle of each.

An interesting observation, which was the cause of considerable concern early in the course of these experiments, was made in connection with the

Cyclops that contained from 8 to 18 larvae. In such individuals several stages of development were frequently represented. For example, fifteen days after the eggs had been fed, mature procercoids and others, representing from three to ten days progress, were present in the same Cyclops. These differences were first considered to be due to the variability in the time at which the eggs had been ingested. The mature forms would thus represent the ingestion of the first eggs, and the less mature individuals the eggs eaten more recently. Further observation, however, indicated that this explanation was incorrect, since it was noted, by examination of the same Cyclops on successive days, that certain of the larvae increased very little in size. Among six *C. fimbriatum* larvae present in one *Cyclops serrulatus*, there were two fully mature, one represented the stage shown in figure 57, and three showed a development of about 10 days. In another Cyclops of the same species containing eight larvae of *C. giganteum*, three were mature (Fig. 68) and five were immature. Their movements after liberation were very feeble and lasted for only five or six minutes. One *Cyclops bicuspidatus* infected with 18 larvae of *Corallobothrium fimbriatum* showed nearly all the stages from the oncosphere to that represented in figure 56. This individual was examined just six days after the eggs were fed (Fig. 51). Many of the Cyclops examined from 25 to 30 days after the feeding of the eggs, showed this same condition of the larvae. This inhibition of growth among the larvae was probably due to the inability of the Cyclops to furnish sufficient nourishment for the complete development of more than three or four individuals.

In connection with the study of the development of *C. giganteum* an observation was made that caused considerable perplexity. In the body-cavity of several Cyclops, along with mature procercoids (Fig. 67), there frequently occurred as many or more very transparent, weakly contractile individuals devoid of hooks and calcareous bodies. They usually measured about 0.10 mm by 0.05 mm (Fig. 63), though one individual measured 0.30 mm by 0.10 mm. This individual was constricted near the middle and presented the appearance shown in figure 61. Kuczkowski (1925) in his study of *I. percae* reports the observation of forms similar to those I have encountered in connection with *C. giganteum*. He offers the suggestion that they represent the cast-off bladders (cercomers) of the mature procercoids. I am inclined to the same conclusion since the size of these transparent individuals is usually about the same as the bladder appendage. Furthermore, the structure of the two is almost identical. In a few instances, however, these peculiar forms were more than twice the size of the attached bladder (Fig. 61). Consequently, if they are accepted as being the bladders that have been separated from the mature procercoids, there must be claimed for them a certain power of independent growth.



A shifting of polarity was noted in the course of the development of the larvae of both species of *Corallobothrium*. During their early phases (from the oncosphere to about ten days), when removed from the Cyclops they moved slowly about with the end bearing the hooks directed anteriorly. Coincident with the differentiation of the scolex at the opposite pole, their polarity was reversed and movements thereafter were made with the scolex-end in advance. This phenomenon was noted also by Janicki and Rosen (1917) in their study of *Diphyllbothrium latum*.

The effects of infection on the Cyclops deserve brief consideration. Infection with a large number of oncospheres (20 to 50) appeared to cause the Cyclops no discomfort. Individuals so infected were quite as active as those unparasitized. Cyclops whose body-cavities contained from 1 to 6 larvae in advanced stages of development disclosed little evidence of any serious effects. When the infection went beyond this point, however, the Cyclops showed evidences of being greatly inconvenienced by the presence of the larvae. An infection as intense as is shown in figure 51 almost totally incapacitated the Cyclops. Such individuals no longer attempted to swim about but settled to the bottom of the fingerbowls and only moved when stimulated with the point of a needle or by vigorous stirring of the water. Then only a few strokes were made with the antennae and abdomen, after which they again settled to the bottom where they remained, apparently dispossessed of every desire for food or action. As has been pointed out by Meggitt (1914) and Janicki and Rosen (1917), such individuals fall an easy prey to the fish which feed on them. However, according to my observations no Cyclops that had been infected in nature contained more than a single proceroid. When it is considered that the chances of a multiple infection are rather slight in a large lake or river, the effect of the parasites on the Cyclops is of relatively little significance.

#### THE SECOND INTERMEDIATE HOST

The experiments in this line were carried on from August 24 to September 9, 1926. Studies on the food of *Ictalurus punctatus*, *Ameiurus melas* and *Leptops olivaris* had shown that minnows and occasionally other species of fish constituted a part of their diet. Copepods were never found in the food examinations of any of the foregoing species. Therefore it seemed improbable that such a high percentage of infection (nearly 70% in the case of *I. punctatus*) could have resulted from the accidental ingestion of infected Cyclops. Consequently no experiments were made on the direct infection of *I. punctatus* through the agency of the Cyclops. I inclined to the belief that infection of the catfish very likely occurred through the ingestion of forms that fed largely on the Entomostraca of the river. Since the Entomostraca were known to comprise a high percentage of the food of minnows, it was evident that some species of minnow might act

as a second intermediate host for the species of *Corallobothrium*. One of the most widely distributed minnows (*Notropis blennioides*) was selected as the first subject. These fish could not be obtained except from the open waters of the streams in the vicinity of the laboratory. About 100 were taken from Rock River on August 24 and placed in the laboratory aquaria, where they remained 12 days before infection experiments were begun. During that time the weaker individuals were eliminated by death and the stronger were left for the experiments. No food was given them except bits of bread and cracker crumbs, on which they seemed to thrive very well.

From among these fish 8 individuals were examined but no larval cestodes were found. Although the findings which resulted from the examination of eight minnows are not considered as final evidence on the presence or absence of larvae in the remainder of the group, they may be taken as a fair index of the degree of infection in that particular school of minnows.

From a culture containing *Cyclops bicuspidatus* 30 to 40 specimens infected with proceroids were removed. These were placed in an aquarium (2' long, 10" wide, 12" deep) containing water about three inches deep. Three of the smaller minnows were selected and placed in the same aquarium on September fourth. Three days later one minnow was examined and three cestode larvae were discovered on the mesentery along the outer wall of the intestine. Very probably there were others that escaped detection because of their extremely small size as they were only 0.2 to 0.4 mm in length, according to the exact degree of contraction (Fig. 60). The two remaining minnows were killed September ninth and preserved in formol for study by the section method.

Another group of three minnows was infected in the manner just described on September second. On the day of my departure from Rockford, September ninth, these minnows were placed in a quart jar containing 3 inches of water in which they remained for about 12 days. One of them died while I was enroute to Urbana. Of the two that remained one was killed October first, but there were no free larvae observed in the body-cavity. Any that may have been present had probably migrated to the musculature of the body-wall. The third individual was placed in an aquarium with a small uninfected *Ameiurus melas*. The aquarium overflowed shortly afterwards, and this gave the minnow an opportunity to escape. An examination of the catfish on April twenty-ninth gave negative results.

Sections prepared from a minnow killed three days after infection showed two larvae in the intestine, one outside of the intestine in the body-cavity, one in the ovary and three in the musculature. These larvae were not encysted (Figs. 65, 69). Since the larvae were found alive in the body-



cavity of the minnows and since a sectioned minnow showed their presence in the lumen of the intestine, in the coelomic cavity near the intestine and in the ovary and musculature of the body-wall, it is concluded that this minnow (*Notropis blennioides*), and probably others, may serve as a second intermediate host for *Corallobothrium fimbriatum*. No experiments other than those already described were made on the life-cycle of *C. giganteum*. However, it is very probable that the developmental cycle of this species closely approximates that of *C. fimbriatum*.

After the conclusion of the experiments just described, I had an opportunity to secure additional data on the life-cycle of *Corallobothrium fimbriatum*. By the use of a specially devised trawl, Dr. David H. Thompson has been able to take small fish which are rarely obtained by the use of ordinary apparatus. In the early part of September, 1927, he secured 32 *Ictalurus punctatus* and shipped them to me alive. These fish measured from 2 to 3 inches in length. Six individuals out of the shipment harbored from 1 to 3 sexually mature *Corallobothrium fimbriatum*. The food of the young *I. punctatus* consists of plankton, insects, and various kinds of debris. It is quite improbable that infection with this cestode occurred in any other way than by the ingestion of copepods that harbored the procercoids. Therefore it was evident from my studies that the infection of catfish with *Corallobothrium fimbriatum* might result either by feeding on minnows which harbored the larvae, or by the ingestion of infected copepods. The evidence for the latter contention seemed quite substantial but further experimentation was necessary to establish the former statement.

To determine whether or not infection with *Corallobothrium fimbriatum* might take place through the agency of a minnow, the following experiment was carried out. From the cestodes obtained from the small *Ictalurus punctatus* a large number of eggs were collected. These eggs were fed October third and fourth to uninfected *Cyclops prasinus*, and the procercoids developed in about 2 weeks. On October nineteenth the Cyclops were placed in an aquarium with two minnows (*Hybopsis storerianus*)\* and I witnessed the ingestion of the Cyclops by the minnows. Two *Ameiurus melas* which had been kept in a laboratory aquarium since November 5, 1926, were used for the next phase of the experiment. No food had been given to these fish from June to September, 1927. Any parasites that they may have had when brought into the laboratory, it seemed reasonable to suppose had disappeared during their confinement. One of them was examined in September and no parasites of any kind were found. On October twenty-sixth the two minnows that had been fed the infected Cyclops were placed in the aquarium with the other *A. melas*. Both minnows were eaten. An examination of the catfish was made November eleventh and 6 larvae were recovered from the intestinal tract. They

\* Identified by Dr. G. K. Noble, American Museum of Natural History.

measured about 0.3 mm in length. When the scolex was evaginated they resembled very closely the larva shown in figure 64*m*, but when the scolex was invaginated they resembled in every respect the proceroid of *Corallobothrium fimbriatum*; so much so that I have no doubt whatever as to their identity. The results of this investigation make possible an explanation of how adult catfish, which do not feed on plankton to any appreciable extent, become infected with *Corallobothrium*.

#### *Plerocercoid Larvae*

As has already been stated, the completion of the growth of the larvae in the Cyclops has been designated as the proceroid stage. Upon entering the next host transformation into the plerocercoid stage is begun. In *Corallobothrium* the first step in this process is the evagination of the scolex. Should the Cyclops infected with the proceroid be ingested by a catfish, development into the plerocercoid begins at once. However, should the proceroid be taken into another fish such as a minnow, which might be considered an accommodation host, the larva migrates from the intestine and takes refuge in the body-cavity or some organ of the second host where it remains until ingested by the definitive host. Little development occurs before it reaches the proper fish. There was close similarity between the larvae recovered from the minnow and the proceroid of *Corallobothrium fimbriatum* taken from the Cyclops. The only differences noted were the appearance of a larger number of calcareous bodies and an excretory bladder which was not observed in any of the proceroids when removed from the Cyclops (Fig. 60). The smallest plerocercoid found in the intestine of the catfish measured about 0.2 mm in length. In this individual, as in all the young plerocercoids, the scolex is the most prominent feature. The body is only a small cone-shaped projection in which no internal organs can be distinguished. Not until the larvae reach a length of about 1 mm is there a distinct resemblance to the adult individual (Fig. 62).

As has already been shown by Table I, no adult parasites belonging to the genus *Corallobothrium* were present among the fish examined from October to April. This was taken as decisive evidence that the adults do not appear before late spring or early summer and disappear entirely in the late fall or early winter. While this study was in progress it was discovered that the fate of the larvae was entirely different. Because of the difficulty of determining accurately the species of the smaller plerocercoids (Fig. 59), no attempt was made to record them according to species. It was found, however, that larvae of both species of *Corallobothrium* were present throughout the year. Therefore in the data recorded below, the total number of larvae present in each fish is recorded without regard to the species. In the examination of 130 *Ictalurus punctatus*, cestodes belong-

ing to any other genus than *Corallobothrium* were encountered only four times. In those instances the parasite belonged to the genus *Proteocephalus*. Since the larval stages of this form would be exceedingly rare, they should not affect very materially the data on the plerocercoids of *Corallobothrium*.

TABLE II  
SEASONAL OCCURRENCE OF CORALLOBOTHRIUM PLEROCERCOIDS  
Data from *Ictalurus punctatus* taken in Rock River

Date		Number Examined	Number Plerocercoids	Average per fish
April,	1926	14	6	0.43
June,	"	10	53	5.3
July,	"	46	150	3.2
August,	"	25	18	0.72
September,	"	6	2	0.33
November,	"	11	23	2.0
December,	"	18	49	3.3
Total		130	301	2.3

These data indicate that the larvae which enter the fish host in the fall remain in the intestine through the winter. Since those found during December and April measured only from 0.5 to 0.8 mm in length, it is evident that little growth takes place during the winter and early spring. This cessation of growth may be due to temperature conditions or to the absence of sufficient nourishment for further development. Unpublished data collected by the Illinois Natural History Survey indicate that *Ictalurus punctatus* feeds very little during the winter. Doubtless both temperature and the lack of food are responsible for the inhibition of growth during this season.

## COMPARISON OF PROTEOCEPHALUS AND CORALLOBOTHRUM

With the exception of the work of Rosen, all of the experimental work on life-histories of fish cestodes has been on species of *Proteocephalus* (= *Ichthyotaenia*). Megitt's description of the development of *Proteocephalus filicollis* in *Cyclops varius* is incomplete in some respects. Briefly stated, he made the following observations: After the ingestion of eggs the oncosphere attaches itself to the wall of the alimentary canal where it remains about a week before breaking through into the body-cavity. After gaining the coelom it takes up a position near the anterior end of the carapace or in the head above the eye. The embryonic hooks gradually disappear. The body becomes covered with highly refractive bodies. The proceroid reached maturity at the end of three weeks. He states that the proceroid is an elongate gray body of variable size, without scolex or neck. The larva is devoid of divisions. Four suckers occur at the anterior end but an apical sucker is absent. The end bearing the suckers is never invaginated during development. No signs of excretory organs were seen.

The development of *Proteocephalus torulosus* in *Cyclops strenuus* and *Diaptomus castor* as described by Wagner is as follows: The oncospheres were observed in the coelom 24 hours after the eggs had been placed in with the copepods. At the end of 48 to 72 hours the larvae measured 20 to 30 $\mu$ . They had settled themselves on or near the intestine. After a short time the larvae began to elongate. At one pole the first trace of the suckers appeared. Circular and longitudinal muscle fibers appeared along with excretory ducts and large calcareous bodies. An invagination occurred at the posterior end which was eventually taken over by the excretory bladder. The proceroid attained a length of 0.5 to 1 mm. It possessed four suckers whose radial muscles were distinct. The scolex possessed neither hooks nor rostellum. It was not set off from the rest of the body. The body was extremely contractile. The cuticula is broken up in a cover of fine hairs and bristles. In some individuals the embryonic hooks were strewn over the posterior half of the body. The excretory system was plainly visible in its entirety and consisted of an excretory bladder and a dorsal and ventral vessel on each side. Wagner makes no mention of a bladder appendage or cercomer.

Kuczkowski's description of the development of *Proteocephalus percae* in *Cyclops strenuus* may next be summarized. In the course of a few days after the infection, the spherical larvae of a diameter of 35 $\mu$ , were observed in the coelom of the *Cyclops*. This larva soon began to grow



and lose its spherical form. A vaculated region appeared within the body mass which the author interpreted as the "lacuna primitiva" of Grassi and Rovelli. At this stage the larva was 41 to 55 $\mu$  in diameter. There was a decided growth in length and an increased contractility. A cercomer appeared from 14 to 21 days after the infection, then the length of the larva was from 138 to 327 $\mu$  and the length of the bladder from 13 to 42 $\mu$ . The bladder was without hooks. These were found on the posterior portion of the larval body. The proceroid possessed four elliptical suckers. No apical sucker was present but a bladder-like protrusion was noted at the apex of the scolex. The figures indicate that the cuticula was smooth. A well developed excretory system was present, also circular and longitudinal muscle fibers. The larva showed the typical calcareous bodies.

A comparison of the developmental phases of the species of *Proteocephalus* just described with those of *Corallobothrium* brings out some rather significant differences. In *Proteocephalus* the bladder appendage or cercomer is entirely wanting in two species according to the descriptions given and rather rudimentary in the third. In *Corallobothrium* the cercomer is a decidedly prominent structure whose length equals one-third that of the body, 40 to 60 $\mu$ , and is never rudimentary. In *Proteocephalus percae* where the bladder has been observed, it shows signs of being rudimentary since in some cases it measures only 13 $\mu$  in length. According to Kuczkowski the cercomer of *P. percae* never bears the embryonic hooks. These hooks are always found on the posterior portion of the body. This condition is likewise true of the other species of *Proteocephalus* which have been described. In *Corallobothrium*, however, they may be confined to the cercomer, divided between the cercomer and the body, or all on the body. In *Proteocephalus* the suckers are differentiated near the anterior end of the larval body without the scolex being set off. The scolex is never completely invaginated. In *Corallobothrium* the scolex is set off early from the the rest of the body (Figs. 57, 70) and soon afterward is completely invaginated. The *Proteocephalus* proceroid bears a close resemblance to the plerocercoid found in the intestine of the final host. This is not true of the proceroids of *Corallobothrium*, in which a decided transformation takes place in the proceroid before the plerocercoid stage is attained (Figs. 58, 59, 68). In every case the *Proteocephalus* proceroid has a greater length than that of the *Corallobothrium* proceroid. In the three species of *Proteocephalus* whose life-cycles have been studied, only one intermediate host is required. The evidence is fairly substantial that at least one species of *Corallobothrium*, *C. fimbriatum*, may use two intermediate hosts for its development. The striking differences in the development of these cestodes, combined with the differences in adult morphology, should be, in



my opinion, sufficient evidence to satisfy the most critical worker that *Corallobothrium* should remain a separate genus.

#### COMPARISON WITH *DIPHYLLOBOTHRIUM LATUM*

The species of *Proteocephalus* have been compared with those of *Corallobothrium* from the point of view of their development. A similar comparison between *Diphyllbothrium latum* and the species of *Corallobothrium* is of interest. As described by Janicki and Rosen, *D. latum* develops in the following manner: The ciliated larva is ingested by *Cyclops strenuus*. Within a few hours the oncosphere has gained the body-cavity of the Cyclops. The larva remains attached by its hooks to the wall of the intestine 10 to 15 days, during which time it loses its contractility. It becomes elongated and at the end of 6 to 8 days development measures 0.10 to 0.15 mm. At the end of from 8 to 12 days the larva shows calcareous bodies, longitudinal and transverse musculature and a strongly developed cuticular covering. On the twelfth day after beginning development the opposite poles of the body show differentiation. By the twelfth to fifteenth day a special bladder appendage with the embryonic hooks upon it is formed. Now the larva measures from 0.35 to 0.40 mm. At the end of 15 to 20 days the larva has attained a length of from 0.5 to 0.6 mm. Then the bladder gradually degenerates and disappears. At the time of the formation of the bladder an evagination occurs at the opposite end. Later this structure is capable of being invaginated. At the end of development in the Cyclops the larva is covered, especially its anterior portion, with bristle-like processes. At this stage the body is highly contractile. The scolex and excretory vesicle are not formed by the larva while in the Cyclops. These two organs make their appearance in the second intermediate host.

The behavior of the oncosphere of *Corallobothrium* in some particulars is decidedly different from that of *D. latum*. In the former the oncosphere does not remain attached to the intestine of the Cyclops by its hooks. The hooks may be seen in action at any time after the oncosphere has gained the body-cavity. Neither does the larva lose its contractility. The development of *Corallobothrium* larvae is much more rapid, as they attain their greatest length at the end of from 6 to 8 days. In *D. latum* the bladder bears the embryonic hooks; but in *Corallobothrium* the bladder may or may not possess the hooks. The scolex and excretory vesicle are not formed in *D. latum* until the larva has developed in the second intermediate host. In *Corallobothrium* the scolex is formed early, by the tenth or twelfth day. The species of the last-named genus do not possess the covering of bristle-like processes noted for *D. latum*. The *Corallobothrium* proceroid is never more than two-thirds the length of the proceroid of *D. latum*. Another interesting difference is found in the

appearance of the excretory vesicle. In *D. latum* this organ does not occur until the plerocercoid stage, but in *Corallobothrium giganteum* it arises during the development in the Cyclops. It was not observed in *Corallobothrium fimbriatum* until the plerocercoid stage. This might be expected since the proceroid development of *C. giganteum* covering 10 to 12 days is more rapid than that of *C. fimbriatum* which takes 14 to 15 days.

Janicki and Rosen never found more than one mature proceroid in the same Cyclops. I have observed as many as three mature proceroids and three individuals representing 10 days development in the same host. The largest number of larvae reported for *D. latum* in a single Cyclops was from 8 to 10. As many as 18 were found in a single host infected with the eggs of *Corallobothrium fimbriatum*.

This comparative study of the Bothriocephalid, Proteocephalus, and Corallobothrium proceroid furnishes evidence indicating an intermediate position for Corallobothrium between the Bothriocephalids and the genus Proteocephalus. First, in the Bothriocephalids the cercomer is always present and nearly always bears the embryonic hooks, but in Proteocephalus it may be wanting entirely. When present, however, it never bears the embryonic hooks. In Corallobothrium the cercomer is always present and it may or may not possess the hooks. Second, the proceroid of the Bothriocephalids bears little resemblance to the plerocercoid, whereas the Proteocephalus proceroid is almost identical to the plerocercoid while the proceroid of Corallobothrium does not bear a close resemblance to the plerocercoid stage. The Bothriocephalids usually require two intermediate hosts, the Proteocephalids only one, while Corallobothrium may or may not use two intermediate hosts.

#### EARLY DEVELOPMENT IN BOTHRIOCEPHALIDS AND PROTEOCEPHALIDS

Observations on the early development of the Proteocephalids are in close agreement with those on *Diphyllbothrium latum*, *Triaenophorus nodulosus*, *Abothrium infundibuliforme* and *Ligula simplicissima*. There are, however, a number of differences that should be considered. The egg of the Proteocephalids when extruded from the uterus, possesses a gelatinous outer covering which enables it to float about for a time before sinking to the bottom of the stream or lake. Within this gelatinous material is found a second membrane (shell) which contains a quantity of granular material and the fully-formed oncosphere which may or may not be invested with a third membrane. The oncosphere of the Proteocephalids is held a prisoner within its membranes until liberated through the agency of the first intermediate host. The egg of each of the Bothriocephalids mentioned above, closely resembles that of the trematodes. A gelatinous covering is absent. The oncosphere may be fully developed before the egg

is extruded from the uterus, as in *Abothrium infundibuliforme*; or an incubation period of varying length may be necessary after the egg is extruded, as in *Diphyllbothrium latum*. When the egg is mature it is composed of an outer shell, which I consider to be homologous with the second membrane of the Proteocephalid egg, and a layer of cells which envelops the oncosphere. This layer of cells is probably homologous with the innermost membrane reported in most Proteocephalid eggs. Contrary to what occurs in the Proteocephalids, the egg of the Bothriocephalid hatches, thus liberating the oncosphere. The layer of cells enveloping the oncosphere may be provided with cilia, as in *D. latum*, or the cilia may be wanting, as in *A. infundibuliforme*.

A comparison of the size of the oncospheres of certain Bothriocephalids and Proteocephalids is given in the following parallel columns.

Bothriocephalids	Size in micra	Authority	Proteocephalids	Size in micra	Authority
<i>Diphyllbothrium latum</i>	22 to 30	Janicki and Rosen	<i>Proteocephalus filicollis</i>	27(estd)	Meggitt
<i>Triaenophorus nodulosus</i>	22 to 24	Rosen	<i>P. torulosus</i>	20 to 30	Wagner
<i>Abothrium infundibuliforme</i>	50 to 60	Rosen	<i>P. percae</i>	28 to 35	Kuczkowski
			<i>Corallobothrium fimbriatum</i>	20	Essex
			<i>C. giganteum</i>	13 to 16	"

It is of interest to note that the first intermediate hosts of the Proteocephalids and Bothriocephalids considered in this paper are found exclusively among the copepods. The species recorded in the following columns have been studied experimentally.

#### PROTEOCEPHALIDS

Parasite	First Intermediate Host	Authority
<i>Proteocephalus filicollis</i>	<i>Cyclops varius</i>	Meggitt
<i>P. torulosus</i>	<i>Diaptomus castor</i>	Wagner
	<i>Cyclops strenuus</i>	
<i>P. percae</i>	<i>Cyclops strenuus</i>	Kuczkowski
	<i>C. serrulatus</i>	
	<i>C. oithonoides</i>	
<i>P. longicollis</i>	<i>Cyclops strenuus</i>	Kuczkowski
	<i>C. serrulatus</i>	
<i>Corallobothrium fimbriatum</i>	<i>Cyclops bicuspidatus</i>	Essex
	<i>C. serrulatus</i>	
	<i>C. prasinus</i>	
<i>C. giganteum</i>	<i>Cyclops serrulatus</i>	Essex
	<i>C. prasinus</i>	

## BOTHRIOCEPHALIDS

Parasite	First Intermediate Host	Authority
<i>Diphyllobothrium latum</i>	<i>Cyclops strenuus</i>	Janicki and Rosen
	<i>Diaptomus gracilis</i>	
<i>Diphyllobothrium latum</i>	<i>Diaptomus oregonensis</i>	Essex
<i>Triaenophorus nodulosus</i>	<i>Cyclops strenuus</i>	Rosen
	<i>C. fimbriatus</i>	
<i>Abothrium infundibuliforme</i>	<i>Cyclops strenuus</i>	Rosen
	<i>C. serrulatus</i>	
<i>Ligula simplicissima</i>	<i>Cyclops strenuus</i>	Rosen
	<i>Diaptomus gracilis</i>	

There may be some significance attached to the fact that *Cyclops strenuus* acts as the first intermediate host of all the Bothriocephalids and three of the Proteocephalids; that *Cyclops serrulatus* is found among the first intermediate hosts of both groups.



### AFFINITIES OF THE PROTEOCEPHALIDS

A study of the life-cycle of organisms has long been used as a guide to their true affinities. Adult morphology alone is not always a reliable criterion of true relationship. Certain forms, the barnacles and ostracods for example, which were thought to be widely separated phylogenetically on the basis of the adult structure, have been brought close together through the discovery of their developmental cycles. The lack of complete knowledge on the life-cycles of the vast majority of the Cestoda has necessitated a grouping based almost entirely on adult morphology. In recent years sufficient data have been gathered on the development of the fish cestodes to justify pointing out certain apparent affinities.

By the discovery of the life-history of *Diphyllbothrium latum* Janicki and Rosen (1917) were able to indicate more fully the relationship between the Digenea and the Bothriocephalids which was first suggested by Leuckart (1886). This is shown by the following points:

1. Similarity of the eggs
2. Existence of a uterine pore
3. Structure of the larvae
4. Two intermediate hosts
5. Resemblance between the miracidium and coracidium
6. Resemblance between the cercaria and the proceroid

On the basis of the points just enumerated, *Diphyllbothrium latum*, *Triaenophorus nodulosus* and *Ligula simplicissima* show a clear affinity to the Digenea. The development of *Abothrium infundibuliforme* as described by Rosen (1918) differs from the three Bothriocephalids just mentioned in respect to the fifth point. Although the egg of *A. infundibuliforme* goes through the process of hatching, it does not give rise to a ciliated larva or coracidium. In this respect it is further removed from the Digenea than the other Bothriocephalids whose life-cycles are known.

Using the points enumerated above as criteria of the relationship between Bothriocephalids and Proteocephalids, the first variation from the usual Bothriocephalid condition is found in *Abothrium infundibuliforme*; the eggs of which show an intermediate position. Since the eggs of the last-named species contain a fully formed oncosphere when extruded from the uterus, they resemble the eggs of the Proteocephalids; but since the eggs of *A. infundibuliforme* give rise to unciliated larvae, they differ from the usual Bothriocephalid condition. Except for the first and



fifth points there is substantial agreement between *Corallobothrium fimbriatum* and the Bothriocephalids. *Proteocephalus percae* agrees on the second, third, and sixth points, but *P. filicollis* and *P. torulosus* differ in all points except the second and third. Therefore, starting with a typical Bothriocephalid such as *Diphyllbothrium latum*, there is a striking series of transitions in arriving at the typical Proteocephalid condition.

The first variation is found in *Abothrium infundibuliforme*; whose larva is unciliated. Next comes *Corallobothrium fimbriatum*, which varies from the former only in the type of egg. Then *Proteocephalus percae* follows, varying from *C. fimbriatum* in the rather rudimentary condition of the cercomer. Finally, in *Proteocephalus filicollis* and *P. torulosus* a condition is reached which differs from *P. percae* in that no cercomer is reported and thereby the resemblance of its proceroid to the cercaria is lost.

On the basis of the scolex, Fritsch (1886) suggested that *Corallobothrium solidum* represented a connecting link between the Bothriocephalids and the Taenias. In the light of the knowledge of the development of the two groups there is much to support his suggestion. La Rue (1914), after a thorough study of the species of the Proteocephalidae, found them closely related morphologically to the Tetraphyllidea. However, in their development the Proteocephalids show a close affinity to the Pseudophyllidea.

## SUMMARY

1. An intensive study has been made of two new species of *Corallobothrium*. Both species are parasitic in *Ictalurus punctatus*, *Ameiurus melas*, and *Leptops olivaris*. Woodland's proposal (1925) to delete the genus *Corallobothrium* has not been accepted. The genus has been retained and the two new species have been designated as *Corallobothrium giganteum* and *C. fimbriatum*. A description is given of the adult anatomy of each parasite. The scolex of *C. giganteum* is subject to wide variation. Amphitypy occurs in the arrangement of the interovarial organs of both species. A new role has been suggested for the excretory system.

2. Particular attention has been paid to the degree of infection and seasonal occurrence of these cestodes in *Ictalurus punctatus*. Among 130 adults of this species nearly 70 per cent harbored one or the other of these cestodes or both. The adult parasites occurred only from spring to fall but the plerocercoid stage was present in the final host throughout the year.

3. The life-cycle of each cestode was studied experimentally. Infection was produced in *Cyclops serrulatus* and *C. prasinus* by feeding eggs of *Corallobothrium giganteum*. Positive results were obtained by feeding the eggs of *C. fimbriatum* to *Cyclops bicuspidatus*, *C. serrulatus*

and *C. prasinus*. The complete development of both parasites in the first intermediate host has been described. The proceroid of *Corallobothrium giganteum* reached maturity in the Cyclops by the twelfth day after the Cyclops had been exposed to the eggs. The development of the proceroid of *Corallobothrium fimbriatum* required from 12 to 14 days.

4. Observations on the feeding habits of Cyclops reveal that organic debris and cercaria are eaten and that protozoa are consumed in large numbers.

5. Cyclops infected with mature proceroids of *Corallobothrium fimbriatum* were fed to minnows (*Notropis blennius*). Larvae were recovered from the body-cavity of the minnows 3 days after feeding. Sections of an infected minnow showed the presence of the larvae in the intestine, within the coelom, and in the musculature.

6. *Ictalurus punctatus* measuring from 2 to 3 inches in length were found to harbor adult *Corallobothrium fimbriatum*.

7. Cyclops infected with the proceroids of *Corallobothrium fimbriatum* were fed to minnows. The minnows were fed to *Ameiurus melas* and the larvae of *Corallobothrium fimbriatum* were recovered from the intestine of *A. melas*.

8. The evidence indicates that catfish may be infected with *Corallobothrium fimbriatum* either by ingesting infected Cyclops or by feeding on infected minnows.

9. A comparison of Bothriocephalid and Proteocephalid development indicates a close relationship between the two groups.

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## EXPLANATION OF PLATES

All figures, except 39 and 41, were drawn with the aid of the camera lucida. The value of the scale projected is indicated in the explanation of each plate. The following abbreviations are used:

<i>cip</i>	cirrus-pouch	<i>ooc</i>	oocapt
<i>dj</i>	ductus ejaculatorius	<i>rs</i>	receptaculum seminis
<i>def</i>	vas deferens	<i>sm</i>	sphincter muscle
<i>exd</i>	excretory vessel, dorsal	<i>tt</i>	testes
<i>exv</i>	excretory vessel, ventral	<i>ut</i>	uterus
<i>fs</i>	foramina secundaria	<i>ull</i>	lateral uterine pouches
<i>ml</i>	longitudinal muscles	<i>utp</i>	uterine passage
<i>mr</i>	muscle rhomboid	<i>utvp</i>	ventral uterine pore
<i>nl</i>	lateral nerve	<i>va</i>	vagina
<i>nr</i>	nerve ring	<i>val</i>	lower vagina
<i>od</i>	oviduct	<i>vi</i>	vitellaria
<i>oot</i>	ootype	<i>vid</i>	vitelline ducts
<i>ov</i>	ovary	<i>vidc</i>	vitelline duct, common
		<i>vir</i>	vitelline reservoir

PLATE I

## EXPLANATION OF PLATE I

The value of the scale projected on each figure equals 0.3 mm.

- FIG. 1. *Corallobothrium fimbriatum*, scolex of adult, toto.  
FIG. 2. *C. giganteum*, apical view of scolex.  
FIG. 3. *C. fimbriatum*, organs of interovarial space, toto-mount. Vitelline ducts are not shown.  
FIG. 4. *C. fimbriatum*, scolex of adult, toto, more expanded than fig. 1.  
FIG. 5. *C. giganteum* scolex, showing apical prominence.  
FIG. 6. *C. giganteum*, fully extended proglottid from near posterior end.  
FIG. 7. *C. giganteum*, protruded cirrus, cirrus-pouch, vagina and vas deferens, toto.  
FIG. 8. *C. fimbriatum*, ovary of immature proglottid, toto.  
FIG. 9. *C. fimbriatum*, ovary of mature proglottid in same chain as fig. 8.  
FIG. 10. *C. giganteum*, dorsal view of the scolex, much contracted, toto.  
FIG. 11. *C. giganteum*, apical view of the same scolex as in fig. 10.  
FIG. 12. *C. fimbriatum*, ovary of immature proglottid, toto.  
FIG. 13. *C. fimbriatum*, ovary of mature proglottid in same chain as fig. 12.  
FIG. 14. *C. fimbriatum*, frontal section of immature segment.  
FIG. 15. *C. giganteum*, expanded scolex, toto.







PLATE II

## EXPLANATION OF PLATE II

The value of the scale projected on each figure equals 0.3 mm. except  
fig. 24, on which it equals 0.1 mm.

- FIG. 16. *Corallobothrium giganteum*, frontal section of contracted scolex showing excretory vessels much reduced in apex.
- FIG. 17. *C. giganteum*, cirrus fully protruded, drawn from living specimen.
- FIG. 18. *C. giganteum*, cross-section near apices of suckers, showing sphincter about suckers and muscle fibers connecting each pair of suckers.
- FIG. 19. *C. fimbriatum*, sagittal section of much contracted scolex.
- FIG. 20. *C. giganteum*, cross-section at level of cirrus-pouch.
- FIG. 21. *C. giganteum*, frontal section of expanded scolex showing distended excretory vessel in apex.
- FIG. 22. *C. fimbriatum*, frontal section of expanded scolex.
- FIG. 23. *C. giganteum*, fully expanded ovary and associated organs, toto.
- FIG. 24. *C. giganteum*, procercoid showing scolex partially protruded.
- FIG. 25. *C. fimbriatum*, ripe proglottid, toto.
- FIG. 26. *C. giganteum*, mature proglottid.
- FIG. 27. *C. fimbriatum*, cross-section.
- FIG. 28. *C. giganteum*, cross-section near posterior limit of suckers showing part of muscle star.







PLATE III

## EXPLANATION OF PLATE III

The value of the scale projected on each figure equals 0.3 mm. except on  
figs. 39, 40 and 41, on which it equals 0.03 mm.<sup>a</sup>

- FIG. 29. *Corallobothrium fimbriatum*, frontal section of mature proglottid.  
FIG. 30. *C. giganteum*, frontal section of scolex contracted as in fig. 10.  
FIG. 31. *C. fimbriatum*, cross-section showing extent of uterus.  
FIG. 32. *C. fimbriatum*, frontal section of dorsal region of mature proglottid.  
FIG. 33. *C. giganteum*, frontal section of an expanded scolex showing the sphincter muscle  
of the suckers as a knob-like structure.  
FIG. 34. *C. giganteum*, drawing made from three frontal sections. The proglottids shown  
here are three segments posterior to those shown in fig. 38.  
FIG. 35. *C. giganteum*, cross-section through scolex near apices of suckers.  
FIG. 36. *C. fimbriatum*, frontal section of vagina and protruded cirrus and cirrus-pouch.  
FIG. 37. *C. giganteum*, frontal section of contracted scolex, sphincter of sucker shaded.  
FIG. 38. *C. giganteum*, drawn from three frontal sections. The excretory vessels are much  
less distended than those shown in fig. 34.  
FIG. 39. *C. giganteum*, reconstruction of interovarial organs.  
FIG. 40. *C. giganteum*, cross-section of dorsal excretory vessel.  
FIG. 41. *C. fimbriatum*, reconstruction of interovarial organs.

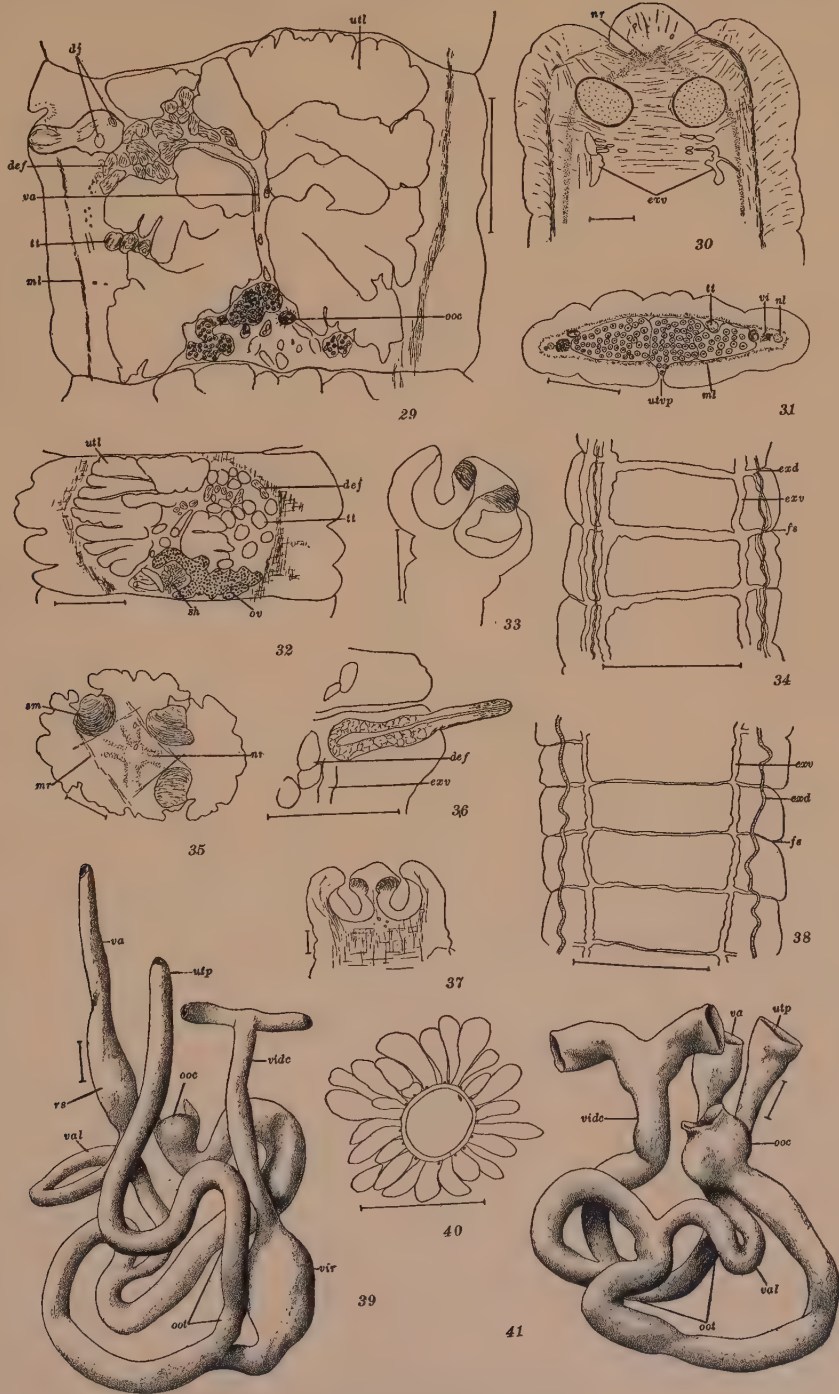




PLATE IV



## EXPLANATION OF PLATE IV

The value of the scale projected on each figure equals 0.03 mm. except on figs. 47 and 51, on which it equals 0.3 mm.

- FIG. 42. *Corallobothrium fimbriatum*, mature egg. The funnel-like cavities at each pole are indicated.
- FIGS. 43 and 46. *C. fimbriatum*, mature eggs in which the middle membrane is ruptured.
- FIGS. 44 and 45. *C. fimbriatum*, oncosphere 10 minutes after being removed from the body-cavity of the Cyclops.
- FIG. 47. *Cyclops bicuspidatus*, containing 8 *C. fimbriatum* larvae 3 days after feeding of eggs.
- FIG. 48. *C. fimbriatum*, larva removed from Cyclops 3 days after feeding of eggs.
- FIGS. 49 and 50. *C. giganteum*, mature eggs.
- FIG. 51. *Cyclops bicuspidatus*, which contained 18 *C. fimbriatum* larvae 6 days after feeding of eggs.
- FIG. 52. *C. giganteum*, tracing of oncosphere seen in the body-cavity of Cyclops 8 hours after feeding of eggs.
- FIG. 53. *C. fimbriatum*, larva seen in abdomen of Cyclops 24 hours after feeding of eggs.
- FIG. 54. *C. fimbriatum*, 4-day old larva.
- FIG. 55. *C. fimbriatum*, 36-hour larva as seen through body wall of Cyclops.
- FIG. 56. *C. fimbriatum*, larva about 10 days old.
- FIG. 57. *C. fimbriatum*, larva from 10-11 days old.

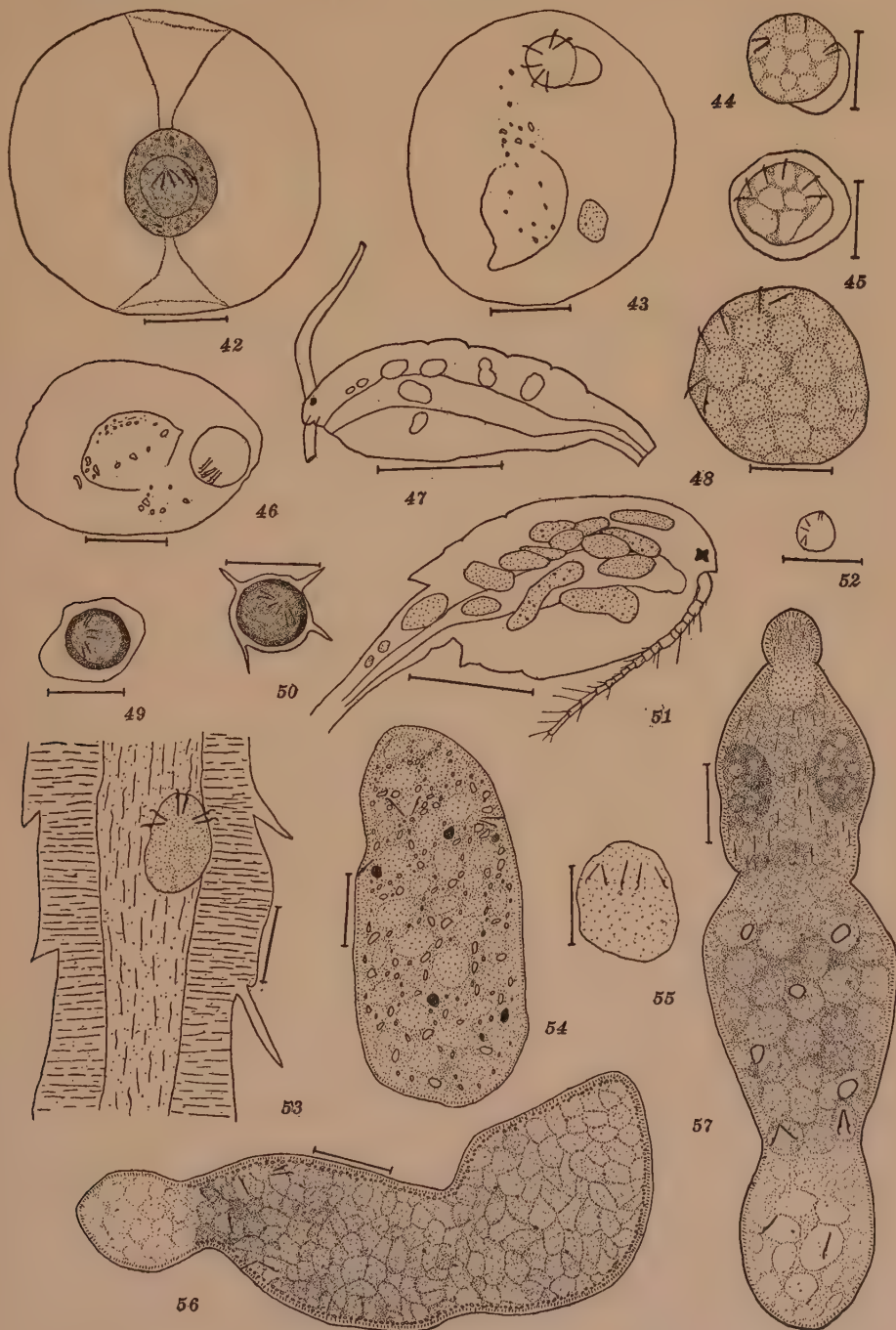




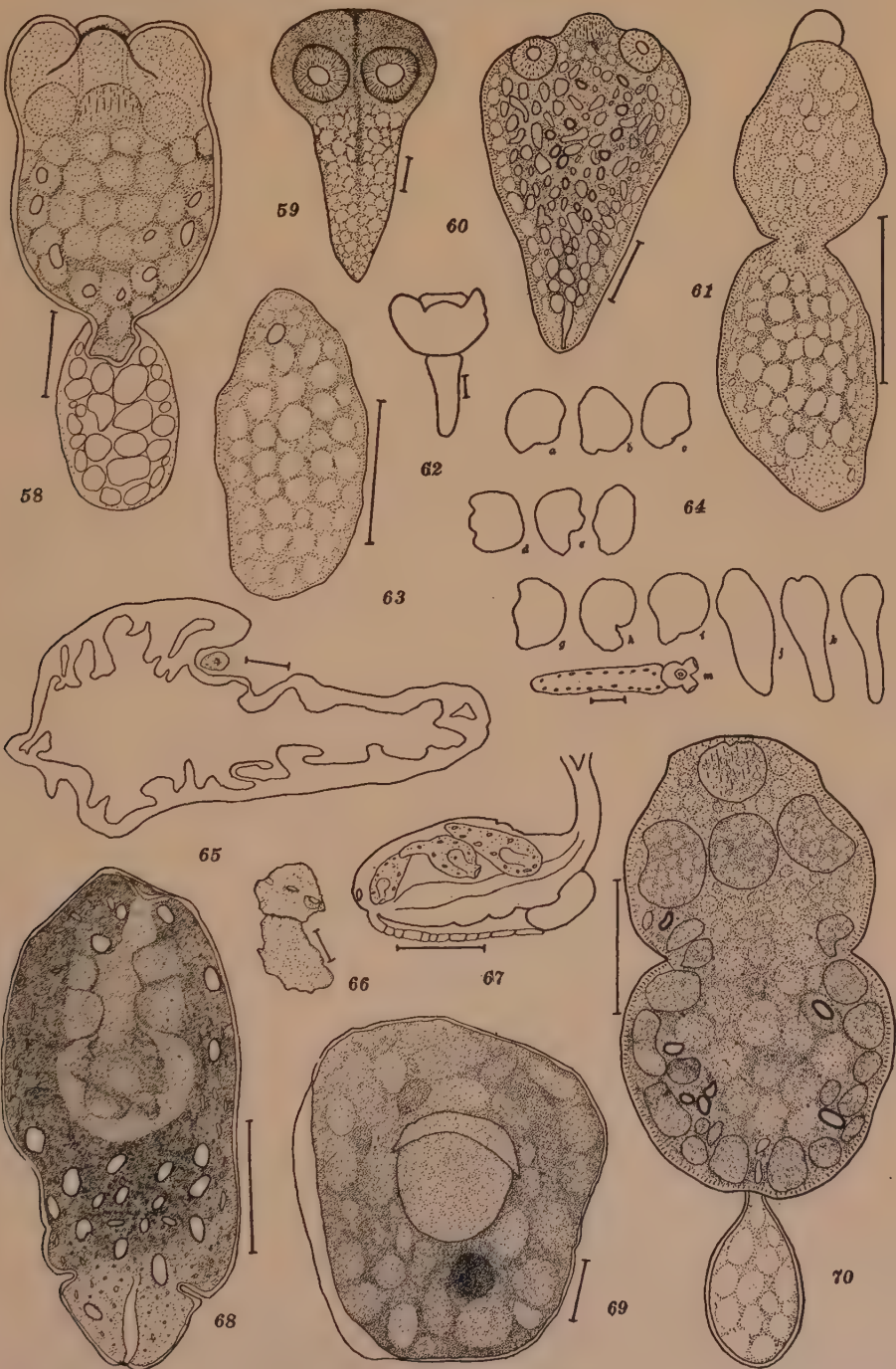
PLATE V

## EXPLANATION OF PLATE V

The value of the scale projected on each figure equals 0.05 mm. except on  
figs. 62, 66, 67 and 69, on which it equals 0.2 mm.

- FIG. 58. *Corallobothrium fimbriatum*, proceroid 12-13 days old with the bladder appendage still attached.
- FIG. 59. Plerocercoid taken from intestine of *I. punctatus*.
- FIG. 60. *C. fimbriatum*, larva somewhat contracted taken from body-cavity of *Notropis blennioides* to which infected Cyclops had been fed.
- FIGS. 61 and 63. *C. giganteum*, forms found in Cyclops which also contained proceroids as shown in fig. 68.
- FIG. 62. *C. fimbriatum*, very young plerocercoid.
- FIG. 64a, b, c, etc. *C. giganteum*, proceroid, outlines indicate shapes assumed before evagination of scolex.
- FIG. 65. *C. fimbriatum*, cross-section of *N. blennioides* intestine with larva outside of intestinal wall.
- FIG. 66. *C. giganteum*, proceroid with scolex evaginated, from preserved material.
- FIG. 67. *Cyclops serrulatus*, containing 3 proceroids of *C. giganteum*.
- FIG. 68. *C. giganteum*, mature proceroid.
- FIG. 69. *C. fimbriatum*, a much enlarged drawing of larva shown in fig. 65.
- FIG. 70. *C. giganteum*, larva from 8-10 days old.





ESSEX

CORALLOBOTHRUM

PLATE V







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# ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XI

October, 1927

No. 4

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## STUDIES ON THE CARYOPHYLLAEIDAE OF NORTH AMERICA

WITH SEVEN PLATES

BY

GEORGE WILLIAM HUNTER, III

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Price \$1.25

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PUBLISHED BY THE UNIVERSITY OF ILLINOIS  
UNDER THE AUSPICES OF THE GRADUATE SCHOOL

DISTRIBUTED, MAY 23, 1930.

# STUDIES ON THE CARYOPHYLLAEIDAE OF NORTH AMERICA

WITH SEVEN PLATES

BY

GEORGE WILLIAM HUNTER, III

Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward  
No. 359

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE  
SCHOOL OF THE UNIVERSITY OF ILLINOIS

1928



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## INTRODUCTION

There have been only a few comprehensive monographs written on the parasites of North American fish. Cooper (1918) adequately dealt with the Pseudophyllidea, omitting, however, the family Caryophyllaeidae. This group of Cestodaria has been given considerable attention during the past few years by several European writers, as Nybelin (1922), Woodland (1923, 1924, 1926), Fuhmann and Baer (1925), and others. On the other hand only four papers have appeared prior to 1925 on the Caryophyllaeidae of North America. Three of these added new species to existing genera and one created a new genus to hold the form described. The writer, therefore, undertook a study of the species found on this continent together with a description of several new species and a consideration of the family Caryophyllaeidae.

The European members of this group have received much attention recently and the abundance of figures and the descriptions of the parasites particularly in the monograph on the Pseudophyllidea by Nybelin (1922), and also Woodland's (1923, 1926) papers bridged the gap where specimens were insecure. Through the kindness of Professor Henry B. Ward the author had access to either slides or vials of original material of all four species described from North America. Dr. Edwin Linton furnished two slides of "*Monobothrium*" *terebrans* and the United States National Museum sent a vial of Linton's "*Monobothrium*" *hexacotyle*. The Museum of Zoology of the University of Michigan sent the type specimen of "*Caryophyllaeus*" *laruei* which was described by Miss Lamont in 1921. Later more of this material was found in vials of Cestodaria which had been sent by Dr. G. R. LaRue to Professor Ward. All of the original material, both slides and vials, for the descriptions of Cooper's (1920) *Glaridacris castostomi* had been added to the collection of Professor Ward and were given to me for further study.

During the past few years over 600 fish from various rivers of the central states known to harbor Cestodaria were examined by the author. A general account and summary of much of the material will be found in a paper by Essex and Hunter (1926). The summer of 1925 was spent in making examinations of living material in the field. The following summer was passed in study at the United States Fisheries Biological Station at Fairport, Iowa, on the Mississippi River. Here over 180 more fish were examined and the living parasites studied. A special trip was taken to Heart Lake, Yellowstone National Park and two trips to Lake Mendota, Madison,

Wisconsin, as well as several trips to the Rock and Illinois rivers in search of additional material. Through the cooperation of other scientists the author has had access to Cestodarian material collected from Minnesota and North Carolina.

In the main the classification followed has been that of Lühe (1910) which has subsequently been modified to include some of the forms encountered which clearly belong here.

The writer wishes to tender his thanks first to the University of Illinois which furnished material and equipment for a summer in the open and to Dr. G. W. Hunter for furnishing further assistance; to the entire staff of the United States Bureau of Fisheries Biological Station at Fairport, Iowa, through whose cooperation it was possible to carry on research work; to the Illinois State Natural History Survey for the loan of equipment and to Dr. D. H. Thompson who supplied many of the fish; to the Zoological Laboratory of the University of Wisconsin for the privileges extended while there; to the United States National Museum for vials of material; to the Museum of Zoology, the University of Michigan for the type specimen of "*C. laruei*"; to the Biological Laboratories of the Rensselaer Polytechnic Institute; and to the following investigators for help: Dr. Edwin Linton, University of Pennsylvania; Dr. H. J. Van Cleave, University of Illinois; Dr. George R. LaRue, University of Michigan; Dr. David H. Thompson, Illinois State Natural History Survey; Dr. Parke H. Simer, Illinois Wesleyan University; Dr. Hiram E. Essex, Mayo Clinic; Dr. Fred J. Holl, University of Buffalo; Wanda Sanborn Hunter, and to others, who, as fellow students have cooperated in many ways, gratitude is expressed.

Particularly to Professor Henry B. Ward the writer wishes to express his sincere appreciation, not only for procuring type specimens, vials of material, loaning much material from his own collection and extending the privileges of his extensive library, but also for the guidance and helpful criticism which has given me the inspiration to complete this work.



## METHODS AND SOURCES OF MATERIALS

The methods used in making this study vary somewhat from those usually employed. First a summary of the sources of material will be given, followed by a description of the methods employed in securing the parasites and finally the methods of preservation and study.

The material in the field was supplied to a large degree by the commercial fishermen. A superficial examination and identification of the host was first made. Later the heads and viscera were supplied for further examination. Such methods permitted a thorough examination of the host, and fish which were unusual in any respect were then secured from the fishermen. This method was employed during the summer of 1925 in the field by Dr. H. E. Essex and myself. The next summer was passed by the writer at the U. S. Fisheries Biological Station at Fairport, Iowa. Here fish were supplied by the crew of the Station who seined them from the Mississippi River, placed them in tubs, and brought them back alive where they were placed in cement lined ponds until examination was possible. As the writer always accompanied the crew on the trips fish were examined as soon as they showed signs of dying.

A third source of material should be noted. The writer made several trips to neighboring streams and by offering to clean the fish that were caught he was able to secure host records and make examinations of numerous viscera for parasites. Through the kindness of Dr. David H. Thompson of the Illinois State Natural History Survey and the cooperation of Mr. "Mike" Hunt fish were shipped on ice to me during the fall and early spring, thus examinations were made which covered nearly the entire year. Through the cooperation of Dr. Parke H. Simer records were secured of hosts taken near Money, Mississippi. Additional material was obtained from Burntside Lake, Minnesota, Lake Erie, New York, and the Eno River, North Carolina.

When in the field the viscera were opened up and macroscopic and microscopic examinations were first made. Then the stomach and intestines were opened, the parasites and the food removed and placed in a normal salt solution pending further study. The intestines were then scraped with a scalpel, the scrapings reexamined under a lens, and the remainder of the visceral mass was examined under a hand lens magnifying 8 diameters. During the summer of 1925 a compound microscope and a portable Spencer dissecting microscope with a maximum magnification of 20 diameters were used. This facilitated the detection of plerocercoid larvae less than 0.5 mm. in length.



Another method employed while in the field should be outlined at this point. The stomachs and intestines were opened, the contents placed in various bottles containing normal salt solutions and labelled "stomach," "upper third," etc. When these were shaken, and the debris decanted off the parasites remained in the bottom of the bottles. A microscopic examination of the stomach and intestines always followed this method. This procedure secured all of the parasites except those 1 mm. or less in size, and is good to use in the field when speed is necessary.

Later a third method was tried. The contents of the stomach and intestine were emptied into a cone shaped plankton net made of bolting-cloth. Another piece of this cloth was placed over the mouth of the faucet to strain out the crustacea, etc. The water was then run through the plankton net; this washed out all of the material except the parasites which were thus concentrated in the bottom of the net. This method may be modified so that the stomach contents are washed first, thus keeping accurate records of the location of the parasites.

After the living parasites were secured they were always placed under the microscope and their methods of movement, type of scolex, length, breadth, translucency, etc. were noted. A study of this nature served to convince me that the scolex possesses certain fundamental characters which are of value in classification. For although the parasites may elongate the scolices nearly 100 percent, the same general shape is usually retained throughout, and if loculi are present they may be seen at all times. On the other hand, there are scolices which are so well formed as to be practically immobile, i. e. *Capingens singularis*. This observation is rather significant when it is found to be generally true in the case of a hundred specimens or more, as was the case with *Hypocaryophyllaeus parataricus*. When it was desirable to keep the parasites alive for some time it was found that they would live up to 72 hours in Ringer's Solution without the dextrose.

#### FIXATION AND PRESERVATION

In the beginning a number of fixatives were tried, but it was soon determined that the best results were obtained after using either Bouins' (picro-formol-acetic), or a saturated aqueous solution of mercuric chloride. These fluids were allowed to act for about 1 to 2 hours and the materials were passed through 50% alcohol and 70% iodized alcohol. Great care must be taken to remove all of the mercuric chloride as otherwise the material will be ruined.

The stain used for toto mounts and sections was Ehrlich's acid hematoxylin and Delafields' hematoxylin mixed half and half. Stains with either one of the reagents mentioned above or with Conklin's modified hematoxylin also gave good results. To secure the best results, however, it was necessary to stain in a full strength solution for several days, destain in

10% acid alcohol (made acid with hydrochloric acid). After destaining the parasites should be transferred to a saturated sodium carbonate solution in 85% alcohol to which had been added 3 to 4 drops of ammonia per 100 cc. In this manner the internal organs could be stained heavily and the outer portions destained rapidly with acid alcohol. The material could then be run up into the clearing agents where it was possible to make drawings before sectioning. Various clearing agents were used, such as benzol, xylol, methyl salicylate (synthetic oil of wintergreen), and cedar wood oil. The last two did not harden the material as much and in the case of embedding it was not necessary to remove all of the cedar wood oil from the paraffin, as was the case with the xylol group. The sections were counterstained with eosin and orange G. One slight change in the usual method of embedding was adopted. The parasite was infiltrated with parawax (melting point about 44 degrees centigrade). This object was then transferred directly to the embedding boat which had just been filled with paraffin of the desired melting point. This gave a block which had an outer hard layer of paraffin while the object itself was filled with parawax, thereby insuring smooth cutting with a minimum of vibration. By following this method excellent sections were secured.

Inasmuch as the testes number is very constant in the adult parasites of this group and varies in the different species from about 50 to over 400, a method for the accurate determination of the number found in any species should be of value. Two methods were employed, depending upon whether the testes were large or small. Both were checked by an actual count of the same and other specimens, so the writer feels warranted in recommending these methods. To secure the best results material which had been cross-sectioned should be used. Furthermore, the number of sections on each row of the slide should be constant.

This first method should be used only when the testes are large so that there are not more than six or eight appearing on a section. Count, by tracing each testis, the actual number of testes in each of ten or fifteen rows. These should be picked at random, care being taken, however, to exclude the first and last rows of sections containing testes. In order to be consistent the testes which were disappearing at the left end of the row were not counted, and any part of a testis showing at the right hand edge was considered as a whole one. The average number of testes of the ten or fifteen rows was taken as the average number per row. The number of rows containing testes was then counted, and this was multiplied by the number found per row. To this was added the actual number found in the first and last rows which contained testes. This method gave very accurate results. It may be checked by the use of sagittal sections, but these are, however, more difficult and less satisfactory.

The second method should be used on forms with small testes where more

than six or eight appear on a section and has been successfully used in estimating the number of testes in cestodes as well as Cestodaria. Count the number of portions of testes visible on each section, add, and divide by the actual number of sections found to contain a single testis. This number should be determined by actually tracing through 30 to 50 testes and taking the average. This method is very accurate for parasites with small sized testes.

#### EXPLANATION OF TERMS

Owing to the fact that there is considerable confusion in the earliest literature regarding the orientation of the body of cestodes and Cestodaria, the writer wishes to explain the terms that will be used in the descriptions which follow.

The terms "lateral" and "marginal" are used synonymously here and correspond to the "marginal" portions of the tape worm strobila, or proglottid. Inasmuch as most Cestodaria are flattened dorso-ventrally this is fairly easy to comprehend. The "ventral" surface is the one upon which the male and female reproductive systems empty, and the "dorsal" surface is, of course, the one opposite. The end of the worm which is devoid of elements of the reproductive system or which bears the scolex, is considered as anterior, and the opposite one posterior. To insure brevity the terms "length," "breadth" or "width," and "depth" are used instead of the longer terms, "diameters in the longitudinal, in the transverse, and in the dorso-ventral directions," respectively. The term "adult" as used herein connotes parasites which show eggs in the uterus. In all the Caryophyllaeidae examined the spermatozoa are formed before the eggs so the presence of the latter presupposes the existence of the former.

## HISTORICAL DATA

The family Caryophyllaeidae was erected by Leuckart (1878) and was first adequately described in 1885 by Claus where it was placed in the tribe Caryophylloidea, along with Archigetidae. The Amphilinae and Gyrocotylidae were placed in another tribe, the Trematodimorpha. Hoyle (1888), in writing for the *Encyclopedia Britannica*, places the Amphilinae, Gyrocotylidae, and Caryophyllaeidae (including Archigetidae as a genus in the latter family) under the order, Monozoa, in contrast to the Merozoa, or polyzootic cestodes. This classification is essentially retained by Benham (1901) in *A Treatise of Zoology* where the class Cestoidea is divided into two grades, "A," the Monozoa and "B," the Merozoa. Then the families Amphilinae, Gyrocotylidae and Caryophyllaeidae are raised to the rank of orders, becoming respectively Amphilinacea, Gyrocotylacea, and Caryophyllacea. Perrier (1897) places Gyrocotyle, Amphilina, Wageneria, Caryophyllaeus, Monobothrium and Diporus in the family Caryophyllaeidae. Lühe (1910) in *Die Süßwasserfauna Deutschlands* separates the Caryophyllaeidae from the Gyrocotylidae and Amphilinae and places them as a family under the Pseudophyllidea which he describes as follows:

Monozootische Pseudophyllideen mit unbewaffnetem und schwach ausgeprägte Saugorgane tragendem Scolex, der von dem folgenden Körper durch eine halsartige Einschnürung abgesetzt sein oder ohne solche direkt in denselben übergehen kann. Ein an seinem Hinterende die Oncosphärenhäkchen tragender Schwanzanhang kann auch beim geschlechtsreifen Tier noch erhalten sein. Genitalorgane nur in der Einzahl vorhanden. Sämtliche Geschlechtsöffnungen flächenständig, ventral, median, dem Hinterende genähert. Cirrus unbestachelt, vor den weiblichen Geschlechtsöffnungen; Vagina und Uterus münden am Grunde eines gemeinsamen Vorraumes, welcher in seinem histologischen Bau dem Genitalatrium ähnelt und sich unmittelbar hinter dem Cirrus in ein nur schwach ausgebildetes Genitalatrium öffnet. Keimstock zweiflügelig, direkt hinter den Genitalöffnungen. Dotterstöcke vor dem Keimstock, in der Markscheid, aber peripher von den Hoden und diese mantelartig umhüllend; eine Gruppe von Dotterstocksfollikeln auch im Hinterende des Körpers, von der Hauptmasse der Dotterstöcke durch den Keimstock und die weiblichen Genitalgänge getrennt. Hoden zahlreich, ausschliesslich vor dem Keimstock und den weiblichen Genitalgängen. Uterus ein geschlängelter Kanal, ohne sackartige Auftreibungen. Eier gedeckelt.

Zwei Gattungen, deren Arten wenigstens im Larvenzustand in der Leibeshöhle von *Oligochaeten* schmarotzen und z. T. dort auch die Geschlechtsreife erreichen.

Cooper in writing concerning the family Caryophyllaeidae in 1920 follows Lühe whose definition he modifies to include his new species, *Glavidacris castostomi*. This was primarily a modification of the scolex characters and reads:

Monozootic pseudophyllidea with scolex unarmed; may or may not bear more or less well expressed sucking organs which are set off from the rest of the body by a neck-like constriction or are fused with the same without such.



Nybelin (1922) makes the family, Caryophyllaeidae, of Leuckart (1878) the subfamily, Caryophyllaeinae, which he places as one of two in the new family Cyathocephalidae. This latter family is characterized as follows:

Pseudophyllideen mit anapolytischer und acraspeder Strobila. Geschlechtsöffnungen flächenständig, median, die desselben Genitalkomplexes stets auf derselben Fläche der Strobila; Mündung des Uterus zwischen denen des Cirrus und der Vagina, in innigster Beziehung zur letzteren. Germarium median gelegen, ausgesprochen zweiflügelig mit lobierten Flügeln; das Gewebe der Seitenflügel viel kompakter als das der Querbrücke. Ootyp von gut ausgebildeten "Schalendrüsen" umgeben. Uterus gewunden, ohne lokale Erweiterung und mit echter Öffnung. Uterinaldrüsen gut ausgebildet. Eier dickschalig, gedeckelt.— Geschlechtsreif in Fischen (Ausnahme Archigetes).

The subfamily Caryophyllaeinae is characterized by Nybelin (1922) in these words:

Cyathocephaliden mit schwach ausgebildeten oder fehlenden Saugorganen am Vorderende, das folglich als Scolex meistens nicht abgesetzt erscheint. Germarium und Geschlechtsausführungswege nur in der Einzahl vorhanden, im hinteren Körperteil gelegen. Hodenbläschen ausschliesslich vor denselben, die ganze Markschrift erfüllend. Vas deferens vor dem Cirrusbeutel gelegen, Prostatastrüsen fehlen. Cirrusbeutelparenchym verhältnismässig bis sehr stark von Muskeln durchsetzt; Cirrus ohne distinkte Wandung. Männliche Genitalöffnung sich der weiblichen anschliessend. Mündung des Atrium utero-vaginale bzw. Ductus utero-vaginalis ohne Sphincter. Vagina in ihrem ganzen Verlauf hauptsächlich nach hinten ziehend. Ausdehnung der inneren weiblichen Genitaleitungswege in der Sagittalebene, hauptsächlich von vorne nach hinten, die Lage derselben annähernd median. Der Germiduct entspringt vom hinteren Rand der Querbrücke des Germariums mit schwach ausgebildetem Schluckapparat, verläuft zuerst nach hinten, biegt dann knieförmig nach rechts oder links um und vereinigt sich mit dem schräg ventralwärts nach hinten verlaufenden Ductus seminalis zu dem sehr kurzen, mehr oder weniger dorsalwärts nach hinten ziehenden Befruchtungsgang. Der unpaare Dottergang verläuft, dorsal von der Querbrücke des Germariums, an der dem Ductus seminalis entgegengesetzten Seite des Germiducts etwas ventralwärts nach hinten und mündet nach einer halbkreisförmigen Biegung ventral in den Befruchtungsgang ein. Dotterstocksfollikel die Hodenbläschen mantelförmig umgebend, eine kleine Anhäufung von Follikeln auch am Hinterende hinter dem Germarium und den Uterusschlingen. Uterus zum grösseren Teil von Uterinaldrüsen umlagert. Eier verhältnismässig gross.

In 1923 Woodland alters his definition of the Caryophyllaeidae to include the species described by Cooper (1920), but places the genus as a synonym of Caryophyllaeus. His redefinition of the family is:

Cestodaria, usually with a slightly flattened cylindrical elongated body but sometimes fluke-shaped, devoid of calcareous corpuscles and cuticular spinelets or hooks, with an anterior end extremely variable in form and size, both in the individual and in different species, which never carries circular suckers but may bear shallow elongated grooves (different in number, form and arrangement to those found in the scolex of other Cestoda), with the cirrus and vagino-uterine apertures contiguous or nearly contiguous on the ventral surface of the body in the median line and occasionally opening into a common shallow atrium, with the testes situated anteriorly and entirely in front of the uterus, with the vagina and uterus forming a complete circuit with a common vagino-uterine opening to the exterior, with a network of excretory channels, the larger ones of which form irregular longitudinal canals about 8 or 10 in number and all of which open externally by a median posterior excretory bladder, and with



a larval form known in some cases to be hexacanth. Parasitic in the intestine of Teleostome fishes (Malacopterygii and Ostariophysi) and in the body cavity of aquatic Oligochaeta (Tubificidae).

This family he places with the Gyrocotylidae in a new order, the Paralinidea, and the Amphilinidae in another new one, the Amphilinidea. Fuhrmann and Baer (1925) point out that the Caryophyllaeidae of Woodland is equal to the subfamily Caryophyllaeninae of Nybelin (1922). They further disagree with Woodland's classification claiming that it is a regression. Woodland, however, in 1926 offers a rebuttal and endeavors to maintain his original classification. Meggitt (1924) in his *Cestodes of Mammals* accepts Nybelin's (1922) classification without change.

#### DISCUSSION

There is little doubt but that there are two sides to the question of the position of the Caryophyllaeidae. It is impossible, however, to settle this question until such time as the life histories of these parasites as well as those of other related groups are better known. Mrázek, for example, in 1908 claimed to have found the larval form of *Caryophyllaeus laticeps* (= *C. mutabilis*) in tubificids. He based this only on the morphological similarities between this form and the adult. Furthermore, he laid considerable stress upon the presence of "faserzellenstränge" which at that time had only been reported for *C. laticeps*. Since then, however, there have been at least three species found which are described as possessing this character. This merely goes to show the indefiniteness incurred when one relies entirely upon morphology. In other words it does not seem logical to point to this with finality until the life histories are completely known. Until that time the decision as to the real position of the Caryophyllaeidae must wait. This will come when the life history of some of the members of the family have been proved and checked beyond doubt. Thus, after more of the life histories of the Pseudophyllidae and several of those of the Caryophyllaeidae have been solved, it will be possible to point more definitely to the true relationship, if any, which may be between them. In closing, however, let me add that the genus *Capingens* certainly shows some Pseudophyllidean characters. The writer, therefore, proposes for the present to follow Lühe, and leave the Caryophyllaeidae as an independent family under the Pseudophyllidae (Hunter, 1927, 1929) rather than accepting Nybelin's (1922) designation as one of the subfamilies of the Cyathocephalidae.

#### THE GENERA OF CARYOPHYLLAEIDAE

The genus *Caryophyllaeus* was described by Gmelin (1790) and *C. piscium* was subsequently regarded as the monotype. This was based on Goeze's (1782) description supplemented by that of Bloch of the same date. Diesing (1850) gives this as a synonym of *C. mutabilis* while von Nordmann

as early as 1840 gives *C. cyprinorum*, *C. mutabilis*, *Fasciola fimbriata* and *Taenia laticeps* as synonyms of *C. piscium*. Rudolphi (1802:98) renames the "*C. piscium*" of Gmelin and Goeze, *C. mutabilis*. Many of the later writers followed this author, for Baird (1853), Blanchard (1888), and Diesing (1850) all used the term *C. mutabilis*. The latter author gives a long list of synonyms in which *T. laticeps* Pallas (1781) is mentioned. Others including St. Remy (1890), Looss (1892), Will (1893), Perrier (1897) and Mrázek (1901) all continue the use of *C. mutabilis*. Will in his paper makes a detailed study of this species and contributes much on the histology and cytology of *C. mutabilis*. Von Nordmann (1840) calls attention to the synonymy of *C. mutabilis* with *C. piscium*, but receives little or no notice. Lühe (1910) gives *C. mutabilis* Rud. (1802) as a synonym of *C. laticeps* (Pallas 1781). Since Rudolphi's account goes back to the "*C*(1) *piscium*" which was first described by Goeze (1782) and Pallas' *T. laticeps* antedates this year, it seems that Lühe has acted correctly. Zeder (1803) added further confusion to the synonymy of *C. laticeps* by describing this same form as *C. cyprinorum* and giving as synonyms *T. laticeps* Pallas and *Fasciola fimbriata* Goeze in *Cyprinus* sp. of Europe. He includes in addition the generic synonyms *Caryophyllus*, *Caryophilinus* and *Phylline*. Two forms were described by Schrank (1788), *Caryophyllinus communis*, and *Caryophyllinus stentoreus*. The first is based on Goeze (1782) and the second on Hermann (1783), but these were relegated to synonymy of *C. mutabilis* by Diesing (1850). More recent workers as Lühe (1910), Nybelin (1922), and Woodland (1923, 1926) have adopted *C. laticeps* (Pallas 1781) and have considered *C. mutabilis* Rudolphi 1802 as a synonym.

According to Baird (1853) there were two forms described by von Siebold, in the collection of the British Museum *C. truncatus* in *Cyprinus nasus* and *C. tuba* in *Salmo fario*. The latter was redescribed as *Ligula tuba*, by Wagener in 1854. Molin (1858) describes "*Caryophyllaeus*" *punctulatus* and "*C.*" *trisinatus* but the figures and descriptions are so indefinite that they are of little value and cannot definitely be placed in this group. Monticelli (1892) suggests that "*C.*" *trisinatus* possesses a tetrabothriid scolex; this was also noted by Woodland (1923). Diesing (1863) created a new genus *Monobothrium* to hold *M. tuba*, the *Ligula tuba* of Wagener, and *M. punctulatum*, the "*C.*" *punctulatus* of Molin. Monticelli (1892) places *M. tuba* (from *Tinca chrysis*) and *M. punctulatum* (from *Conger vulgaris*) in the genus *Caryophyllaeus*. The differences as noted by Diesing (1863) were previously denoted by Wagener and subsequently by Monticelli as being specific, rather than generic. Since that date many papers have appeared dealing primarily with descriptions of various species.

The genus *Archigetes* was erected by Leuckart (1878) to hold a Cestodarian, "*C.*" *appendiculatus*, found by Ratzel (1868) in tubificid worms; he renames this form *Archigetes sieboldi*. Gruber (1881) describes the repro-

ductive system of *A. sieboldi*. Mrázek (1897) made a careful study of this form and added much histological and embryological data. It is unfortunately written in Hungarian, and is, therefore, inaccessible to most of the world. The same author in 1908 described another member of this genus, *A. brachyurus*, also found in the body cavity of the Tubificidae. Wisniewski (1928) briefly described a new species, *A. cryptobothrius*, from the body cavity of *Limnodrilus hoffmeisteri*.

The genus *Lytocestus* was erected by Cohn (1908) to hold a new Cestodarian, *L. adhaerens*. Since that date Woodland (1923, 1924) described two species which belong here, *L. filiformis* and *L. chalmersius*, as members of the genus *Caryophyllaeus*. The same writer (1926) refers "*C.*" *indicus* (Moghe 1925) to this genus and the "*Monobothroides*" *cunningtoni* of Furhmann and Baer (1925), as well as a form described by Johnston (1924) as "*Balanotaenia*" *bancrofti*. Nybelin (1922) in his monograph on the Pseudophyllidea reviews the literature on the Caryophyllaeidae and retains the genera *Monobothrium*, *Caryophyllaeus*, *Archigetes* and establishes a new one, *Caryophyllaeides*, to hold Schneider's "*C.*" *fennicus*. Woodland (1923) found it necessary to create the genus *Wenyonia* to take care of three new species, *W. virilis*, *W. acuminata* and *W. minuata*. In 1924 Kulmatycki redescribed *W. virilis* as "*Caryophyllaeus*" *noliticus*. Fuhrmann and Baer (1925) described a new genus and species which they called *Monobothroides cunningtoni*. Bovien (1926) described six new species of *Caryophyllaeus*, *C. javanicus*, *C. oxycephalus*, *C. serialis*, *C. tenuicollis*, *C. microcephalus* and *C. acutus*. This same author also described one new genus and species, *Djombangia penetrans*. As pointed out in a previous paper (Hunter 1929) further study of these six species will undoubtedly bring about a reclassification of these parasites which will place them in the *Lytocestinae*. Motomura in 1927 added another new species, *C. gotoi*. Baylis followed this in 1928 with a new genus and species, *Lytocestoides tanganyikae* which he tentatively places in the *Lytocestinae*.

In America progress has not been so rapid. Linton (1893, 1897) described two species of Caryophyllaeidae as "*Monobothrium*" *terebrans* and "*M.*" *hexacotyle*. Ward (1911) records the presence of *Archigetes* in North America and Cooper (1920) erects a new genus, *Glaridacris*, to hold his species, *G. catostomi*. Lamont (1921) followed this with a description of "*C.*" *laruei*. Essex and Hunter (1926), in a joint paper, record the presence of Cestodaria in various fresh water fish. Hunter (1927) published a brief redescription of the American forms and added three new genera and four new species, *Capingens singularis*, *Biacetabulum infrequens*, *Hypocaryophyllaeus paratarius* and *Monobothrium ingens*. This was followed in 1929 by the description of two new genera and five new species, *Pseudolytocestus differtus*, *Spartoides wardi*, *Glaridacris confusus*, *Biacetabulum meridianum* and *B. giganteum*.



Some of the more important general papers should be mentioned. Fraipont (1880) wrote concerning the excretory apparatus of the trematodes, cestodes and Cestodaria. In 1890 St. Remy considered certain aspects of the reproductive system of *C. laticeps* (= *C. mutabilis*). Pintner (1880) discusses the situation in the Cestodaria, and D'Udekem (1855), mentions two scolices found in Tubificidae. The homologies of the female genital organs of trematodes and cestodes were treated by Odhner (1912). Loennberg (1897) in his paper attempts to show that the Caryophyllaeidae are secondarily monozootic whereas the Gyrocotylidae are primarily so, or as he puts it, "primatively" so. This dissertation was followed in 1905 by Spengel's paper on *Die Monozootie der Cestoden*, and by Cohn (1907) on the orientation of the cestodes.

Stiles and Hassall did much to simplify the compilation of a working bibliography by their publication of the section of the Index-Catalogue of Medical and Veterinary Zoology on Subjects: Cestoda and Cestodaria.

#### DISCUSSION OF THE GENERA OF THE CARYOPHYLLAEIDAE

##### *The Caryophyllaeus Group*

The problem under discussion is not the old characterizations of the genera, for those have of necessity changed to keep pace with the advances in scientific knowledge, but deals with the genera proposed as valid by more recent workers. Since there may be fourteen or fifteen genera in the family Caryophyllaeidae it will be rather difficult to cope with all in detail. The genera Archigetes Leuckart 1878, Lytocestus Cohn 1908, Wenyonia Woodland 1923 appear to be accepted as valid by most workers today. The genera which will be considered are Caryophyllaeus, Monobothrium, Glaridacris and Caryophyllaeides; these have been placed by Woodland (1923, 1926) in one genus, Caryophyllaeus.

First a comparison of the characters of several of the genera considered by Nybelin (1922) will be made. He characterized the genus Caryophyllaeus as follows:

Caryophyllaeinen mit mehr oder weniger verbreitertem, dorsoventral abgeflachtem, sogar gekräuseltem Vorderende, ohne jede Spur von Saugorganen. Wassergefäß-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig stark gewunden, ohne Vesicula seminalis externa. Cirrusbeutel gross, eiförmig, Ductus ejaculatorius ohne distinkte Wandung. Mündungen von Cirrus und Ductus utero-vaginalis dicht hinter einander in einer seichten, anscheinend nicht vorstülpbaren Genitalcloake. Ductus utero-vaginalis lang. Vagina mit grossem Receptaculum seminis und sehr engem, vom Receptaculum scharf abgesetztem Ductus seminalis. Germarium H-Förmig, Germiduct verhältnismässig lang, aber nicht auffallend weit, median entspringend. Uteruswindungen nie vor dem Cirrusbeutel.—Geschlechtsreife im Darm von Cypriniden. Procercoistadium, soweit bekannt, in Tubificiden.

This is followed by the description of Monobothrium:

Caryophyllaeinen mit trichterförmig einstülpbarem, in ausgestrecktem zustande sechskantigem, mit zwei flächenständigen, sehr schwach ausgeprägten bothrienähnlichen

Vertiefungen versehenem Vorderende. Wassergefäß-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig stark gewunden, ohne Vesicula seminalis externa. Cirrusbeutel verhältnismässig klein, birnförmig, Ductus ejaculatorius mit distinkter Wandung. Mündungen von Cirrus und Atrium utero-vaginale zusammen in einer seichten, vorstülpbaren Genitalcloake, jedoch von einander durch einen, die Cirrusöffnung umgebenden, voluminösen Ringwulst (männliche Genitalpapille?) ziemlich weit getrennt. Atrium utero-vaginale breit. Vagina ohne Receptaculum seminis und scharf abgesetzten Ductus seminalis. Germarium H-förmig, Germiduct verhältnismässig lang und sehr weit, nicht median, sondern rechts oder links von der Mittellinie des Germariums entspringend. Uteruswindungen nie vor dem Cirrusbeutel.—Geschlechtsreif im Darm von Cypriniden. Entwicklung unbekannt.

Nybelin creates a new genus to hold the form described by Schneider (1902). He names this genus *Caryophyllaeides* and characterizes it in the following words:

*Caryophyllaeinen* mit quer abgestumpftem, kaum merkbar verbreitertem Vorderende ohne jede Spur von Saugorganen oder Kräuselung. Wassergefäß-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig schwach gewunden, ohne Vesicula seminalis externa. Cirrusbeutel gross, eiförmig, Ductus ejaculatorius ohne distinkte Wandung. Mündung des Cirrus am inneren Ende des weiten, aber nicht besonders langen Ductus utero-vaginalis. Vagina mit wohlausgebildetem, vom Ductus seminalis aber nicht scharf abgesetztem Receptaculum seminis. Germarium mit sehr langen vorderen und dorsal sich vereinigenden hinteren Schenkeln der Seitenflügel, Germiduct kurz und sehr eng, median entspringend. Uteruswindungen zum grössten Teil vor dem Cirrusbeutel.—Geschlechtsreif im Darm von Cypriniden. Entwicklung unbekannt.

Cooper (1920) describes a fourth new genus, *Glaridacris*, as follows:

With the characters of the family. Medium sized caryophyllaeids with the anterior end modified to form a scolex, provided on each surface with three suckers, of which the median one is the deepest and most efficacious. Main longitudinal parenchymatous muscles in eight large fasciculi in the anterior part of the neck and the base of the scolex. Only two main nerve strands in the medulla, connected in the scolex by two more or less diffuse commissural loops. Excretory vessels form a single cortical plexus with eight principal longitudinal channels; no true flame-cells present, terminal renal organs, peculiar, highly vacuolated, simple cells. Expansion of the vas deferens before entering the cirrus-sac to form a vesicula seminalis . . . .

Woodland (1926) deletes the last three of these genera and places them in the genus "*Caryophyllaeus*" which he describes as:

*Caryophyllaeidae* with the sexual apertures situated within the last quarter of the body-length, and the ovary near the posterior extremity. The longitudinal extent of the uterus is at the most one-third of that of the testes and usually much less. Two layers of longitudinal muscles fibres, one lying external to the nuclear layer of the subcuticula and just internal to the "Stäbenschicht"—the subcuticular layer—and one separating the medullary from the cortical parenchyma—the epi-medullary layer. The vitellaria are medullary, have a more or less annular arrangement round the testes, and are in part situated behind the ovary. The ovary is in the medulla. The uterus wall is in large part invested by a thick layer of gland-cells—the uterine glands. Parasitic in the intestines of the Cyprinidae.

The question then is whether Woodland is warranted in so doing. Should these forms really be confined in one genus or was Nybelin right in maintaining *Caryophyllaeus*, *Monobothrium* and *Caryophyllaeides* as three distinct genera? It should be borne in mind that taxonomy at the best



is pragmatic. In the opinion of the writer it should be employed to simplify the work of classification and not to complicate it. The means of securing this end is largely a matter of personal opinion. The decision can be reached after a careful examination of the points upon which they are based. Woodland maintains his genera largely upon the position of the musculature in relation to the reproductive organs, a character undoubtedly valid, but one which is of more than generic value. Furthermore, the inner longitudinal muscles which separate the medullary from the cortical parenchyma are always readily distinguishable. The one "lying external to the nuclear layer of the subcuticula and just internal to the 'Stäbenschicht' the subcuticular layer," (called the outer longitudinal layer by this author), is not always as readily found as the former, and in fact is sometimes absent except in the neck region. It is doubtful, therefore, if this character can be used (in its entirety) with as great facility as Woodland intimates. The position of the sexual aperture and ovary is considered by both Nybelin (1922) and Lühe (1910) as a family character. The former speaks of it directly and the latter denotes the genital opening as "approaching the posterior end" and later speaks of the ovary as being behind the genital opening. It should be realized that this character would have to be altered since the description of Woodland's genus, *Wenyonia*, appeared in 1923, but this point will be discussed in detail later. Woodland's second character of the genus dealing with the longitudinal extent of the uterus in relation to the length of the testicular field does not hold, for the figure of "*C.*" *skrjabini* clearly shows the uterus extending longitudinally for more than one-third the length of testes. The fourth character, regarding the annular arrangement of the vitellaria is not valid for in the case of *G. hexacotyle* they are confined to two lateral rows while in *Monobothrium ingens*, Hunter (1927) there are no post-ovarian vitellaria. This merely goes to show that even Woodland's characterization of the genus *Caryophyllaeus* is also subject to change as other forms are described, a fact which no one could foresee and one which Woodland hoped to avoid.

Having considered Woodland's description of *Caryophyllaeus* we can now turn to Nybelin's. This author goes to the other extreme and includes characters which are really of specific rather than generic value. For example, the length of the utero-vaginal duct is not to be compared in value to the shape of the ovary, or the position of the uterine coils with reference to the cirrus sac. It is equally clear that several other characters, as the type and windings of the vas deferens, or the presence or absence of a distinct wall in the ductus ejaculatorius are not of generic importance. However, certain other characters as type of genital atrium, shape of ovary, position of the uterine coils in relation to the cirrus sac and the presence or absence of an external seminal vesicle are undeniably of generic import.

The same general criticism has been made by Woodland (1926) of the

genus *Caryophyllaeides*, the only difference being that he does not admit the existence of other characters of generic importance. A similar situation prevails with the genus *Monobothrium*, for here again Nybelin includes a number of characters which in the opinion of the writer are subgeneric.

There are then the two extremes, Woodland on the one hand advocating the deletion of *Monobothrium*, *Glaridacris* and *Caryophyllaeides* in order to secure a genus which is composed of "relatively deep-seated and easily recognizable characters, are as concise as is consistent with precision, and are not likely to require serious amendment in the near future." On the other extreme as we have seen above is Nybelin who delves deeply into the minute anatomical characters of the different species. But if the latter's characterization of the genera is fundamentally sound other species should fit into the genera already created. The description of Popoff's (1924) "*C.*" *skrjabini* places it as another member of Nybelin's genus *Caryophyllaeides*, provided that some of the characters which have been termed "specific" by Woodland and this author are omitted and only the main characters retained. Such are the characters relating to the type of scolex, the presence of the inverted "A" shaped ovary, the presence of an external seminal vesicle and the position of the uterine coils anterior to the cirrus sac. There would then be two species in this genus. In a previous paper the writer (Hunter, 1927) describes a new species, *M. ingens*, which falls into the genus *Monobothrium* provided the same type of characters are used and the specific ones deleted. Then the genus would be characterized by the scolex, the position of the uterine coils in relation to the cirrus sac, shape of ovary, type of genital atrium, presence of an external seminal vesicle and the presence or absence of post-ovarian vitellaria. In a similar fashion two other species originally placed in *Monobothrium* and *Caryophyllaeus* respectively were shown to belong in the genus *Glaridacris*, these being *G. hexacotyle* and *G. laruei* (see Hunter 1927).

These examples serve to show that the genera may be retained. The question of whether a character be specific or generic is after all largely a matter of opinion. The generic characters listed above are as easily determinable as those denoted by Woodland in his description of the genus *Caryophyllaeus*, and the writer agrees with Woodland that they should be of such a facilely determinable nature, if possible. It seems, however, that such features could be readily distinguished by persons unacquainted with the group and therefore would have the same advantage claimed by Woodland for his classification. He says, "Above all, they possess [speaking of the genera *Caryophyllaeus*, etc.] the advantage that persons unacquainted with this group can, without difficulty, relegate a new or unknown species to its appropriate genus, and therefore possess the maximum of utility." As Woodland says classification is largely a matter of convenience and utility. Surely it would be simpler and infinitely easier to determine whether a spec-

ies were new by having several well defined genera each containing a few species rather than one with many. If Woodland's scheme is followed there would be 15 or 18 species in the genus *Caryophyllaeus* instead of three, four or more equally well defined genera with fewer species in each. Furthermore classification should primarily show relationships, setting apart those groups which differ. The genus *Monobothrium* was originally erected by Diesing (1863:228) to hold species which were different from those in the genus *Caryophyllaeus*. This group was deleted by Monticelli (1892), but later was restored, after further study of the same species, by Nybelin (1922). Once a genus has been created it should be retained if it is valid. Both Nybelin (1922) and the present author have shown its validity, and Fuhrmann and Baer (1925) as well as Meggitt (1924) have accepted Nybelin's diagnosis of the genera. The writer proposes, therefore, to retain the genera *Caryophyllaeus*, *Monobothrium* and *Caryophyllaeides* as well defined genera. Their characters, however, will of necessity be modified according to the preceding paragraphs.

The genus *Glaridacris* as described by Cooper (1920) is of little value for he makes use of characters difficult to ascertain with any degree of accuracy. It is also unsatisfactory because it does not employ the characters which are used by other workers. The difficulties are shown in the following: the first character is denoted as "With characters of the family," and might well be summed up by saying "*Caryophyllaeidae*"; the division of the inner longitudinal muscles into 8 fasciculi is specific rather than generic; the presence of two main nerve strands is true of all those forms which have come under my observation and probably is a family or class character; the number of main longitudinal excretory canals has been found to vary in an individual from 6, 8 to 10, or from 8, 10 to 12. The present writer also hoped to be able to make use of this character but could not. The sixth character designating the existence of renal corpuscles instead of flame cells is too difficult to be generally used. It has the further disadvantage of being a cytological rather than a morphological distinction. The characters of the scolex and the presence of an external seminal vesicle are important and of value. In other respects it closely resembles the genus *Caryophyllaeus* except for the fact that so far it has been found only in the *Catostomidae*. If this genus were retained it would hold four species. The validity of this genus may be questioned by some since its present existence depends to a large degree upon three characters, the scolex, the presence of an external seminal vesicle and the host. But upon examining the literature we find evidence of genera being retained as valid when there is only *one* distinguishing character. In the *Proteocephalidae* the genus *Corallobothrium* differs from the genus *Proteocephalus* in the type of scolex. To be sure, Woodland (1925) has advocated the deletion of the genus along with several others, but Essex (1928) and other workers contend that it should be retained.



Furthermore, Fuhrmann (1916) created the genus *Goezeella* upon the basis of the scolex alone (in which respect it differs from *Monticellia*). Therefore since other genera have been retained upon one character and there are here three points of difference it is evident that the genus *Glaridacris* should be retained as valid.

The writer has endeavored to show in the preceding paragraphs that the following genera should be retained: *Caryophyllaeus*, *Monobothrium*, *Glaridacris*, *Caryophyllaeides* and three which were not discussed, *Archigetes*, *Lytocestus* and *Wenyonia*. The first four may be characterized by type of scolex; type of genital atrium, (i. e. whether the cirrus opens into the utero-vaginal canal, or whether there are two separate orifices etc.); shape and position of ovary (whether medullary or cortical); position of uterine coils in relation to cirrus sac; presence of post-ovarian vitellaria; position of vitellaria in relation to inner and outer longitudinal muscles; the presence or absence of an external seminal vesicle; host.

The genus *Archigetes* is described by Nybelin (1922:134) as follows:

Caryophyllaeinen mit verjüngtem und dorsoventral abgeflachtem oder sechskantigem, stets aber mit zwei flächenständigen, anscheinend gut ausgeprägten, bothrienähnlichen Vertiefungen versehenem Vorderende. Wassergefäß-System nicht mit einer einzigen Endblase, sondern mit zahlreichen Ampullen am Hinterende des Körpers. Vas deferens sehr schwach gewunden, mit birnförmiger Vesicula seminalis externa. Cirrusbeutel verhältnismässig klein, rundlich, Ductus ejaculatorius mit distinkter Wandung. Cirrus in den Ductus utero-vaginalis mündend. Vagina ohne oder mit nur schwach differenziertem Receptaculum seminis und Ductus seminalis. Germarium hantelförmig, Germiduct median entspringend. Uteruswindungen wenig zahlreich, zum kleineren Teil auch vor dem Cirrusbeutel.—Geschlechtsreif mit zeitlebens erhaltenem, die Embryonalhäkchen tragendem Schwanzanhang in der Leibeshöhle von Tubificiden.

Undoubtedly a more detailed study of this group will disclose several new genera. However, the generic characterization remains broader if the cirrus sac, ductus ejaculatorius and the oviducal characters are omitted. The others are valid, but in the opinion of the writer, are specific rather than generic in character.

#### *The Lytocestus Group*

The genus *Lytocestus* is described by Cohn (1908:139) in these words:

Scolex unbekannt. Frühe Loslösung der Proglottiden, keine Differenzierung an deren Haftende. Keine präformierte Uterusöffnung; ♂ und ♀. Genitalporus hintereinander, flächenständig. Hoden zahlreich in der Marksicht; Ovarium zweiteilig mit medianem Reservoir, Dotterstöcke in der Rindenschicht, ringförmig, Schalendrüse neben dem Ovarialreservoir. Im Darne von Fischen.

Later Woodland (1926: 56) describes the genus as:

Caryophyllaeidae in which the position of the sexual apertures and ovary and the relative longitudinal extents of the uterus and testes are as in *Caryophyllaeus*. The longitudinal muscles consist of two layers, as in *Caryophyllaeus*, but the outer layer (the cortical layer) is internal to the nuclear layer of the subcuticula and not external to it. The vitellaria are

cortical, have an annular arrangement round the testes, and are wholly absent behind the ovary. The follicles of the ovary are cortical, only the median receptacle and the proximal portions of ducts being medullary. Uterine glands present. Parasitic in intestines of Mormyridae and Siluridae."

In the light of our present knowledge it is apparent that Woodland's (1926) description of the genus goes to the same extreme as does his characterization of *Caryophyllaeus*. This raises the question of whether or not he is using characters which are of greater than generic value. Cohn (1908), although his description is inadequate, goes into too much detail and like Nybelin, uses subgeneric characters. The genus *Lytocestus* can be maintained on the basis of scolex character, type of the male and female genital pores, presence or absence of post-ovarian vitellaria, relation of the longitudinal extent of the uterus to that of the testes, shape of the ovary and the host. This leaves many of Woodland's (1926) characters unused. The reasons for this will appear in subsequent paragraphs.

Fuhrmann and Baer (1925) describe a new species of Cestodarian which they place in a new genus and species, *Monobothroides cunningtoni*. Certainly it is related to the genus *Lytocestus* and according to Woodland it should be considered as a synonym of this genus. However, in this author's revision of *Lytocestus* the genus *Monobothroides* differs from it primarily in the type of scolex. This character alone is perhaps sufficient grounds for maintaining the genus, but before the question can be definitely settled the writer feels that the original description of Cohn's (1908) *L. adhaerens* should be amplified. Inasmuch as *Monobothroides* is probably valid it should be left as a genus until it is definitely proved to belong elsewhere, and if further study shows the genus to be valid, the author believes that *L. chalmersius* may be found also to belong in the genus *Monobothroides*.

#### *The Wenyonia Group*

The genus *Wenyonia* was added to the *Caryophyllaeidae* in 1923 when it was originally tersely described by Woodland (1923:455) in these words:

The sexual apertures situated in the anterior half of the body. The longitudinal extent of the uterus is at least equal to that of the testes. Parasitic in the intestine of Siluridae.

Three years later (1926:59) the definition was amplified so that it read:

*Caryophyllaeidae* in which the sexual apertures are situated in the anterior half of the body. The longitudinal extent of the uterus is at least equal to that of the testes. The longitudinal muscles may consist either of one thick layer occupying the whole cortex, or this may become split into two layers resembling those of *Lytocestus*. The vitellaria are medullary, are restricted in position to two lateral narrow tracts, and extend behind the ovary. The entire ovary is medullary. Uterine glands are absent. Parasitic in the intestines of Siluridae.

It is the belief of the author that a subsequent study of this group will make it possible to make more use of the same type of characters so typical of the *Caryophyllaeus* group. However, for the present the genus may be



characterized by scolex, longitudinal extent of the uterus, position, shape and type of the ovary, non-reduced ovarian commissure, presence of a terminal excretory bladder and the host.

The writer has attempted to show that the three groups of Caryophyllaeidae are distinct and yet are warranted in being subdivided into more than the one genus proposed by Woodland (1926). It is evident, however, from Woodland's account and figures that these three "genera" are fundamentally different. Yet Nybelin, Fuhrmann and Baer and the present writer have all pointed out how these groups may be subdivided into their respective valid genera. Furthermore, the genera in the Caryophyllaeus group, Caryophyllaeus, Monobothrium, Glaridacris, Caryophyllaeides and Archigetes, are undeniably more closely related to each other than to such forms as Lytocestus and Wenyonia. For example, both Monobothrium and Caryophyllaeus have vitellaria which are medullary and surrounded by the inner longitudinal muscles, their sexual apertures are within the last quarter of the body length, and uterine glands are present. They conform, in other words, to some of Woodland's characters, but they differ from Lytocestus in the location of the vitellaria in relation to the inner longitudinal muscles. These two genera differ markedly from Lytocestus and yet are fairly close to Woodland's definition of Caryophyllaeus. Since classification is meant to show relationships and a study of this group has shown the existence of the Caryophyllaeus, Lytocestus and Wenyonia groups, which have been sensed by Woodland (1926:63) when he says "that the three genera—Caryophyllaeus, Lytocestus, and Wenyonia—above defined by me are as distinct from each other as are any three genera contained in any other family of the Cestoda,"—the writer (1927) erected three subfamilies, the Caryophyllaeinae, Lytocestinae and Wenyoninae to hold the three groups of related genera.

The family Caryophyllaeidae would then be retained as the only family of the monozootic Pseudophyllidea, which in turn would contain Nybelin's (1922) subfamily Caryophyllaeinae (=Caryophyllaeidae Lühe) with modified characters, and the two new subfamilies, Lytocestinae and Wenyoninae. A brief account was published in 1927. This necessitates taking the subfamily Caryophyllaeinae of Nybelin (which is equal to the family Caryophyllaeidae of Lühe (1910)) out of the family Cyathocephalidae and placing it back by itself as a family of monozootic Pseudophyllidea.

#### THE CAPINGENS GROUPS

During the preparation of this monograph several genera were found which clearly belonged to still another group. The genus Capingens described by the author in 1927 was placed in the Lytocestinae on the basis of the relation of the musculature to the vitellaria. It was noted at the time that the vitellaria were not *entirely* cortical to the inner longitudinal muscles,

but instead had their origin within the muscle band (i. e. medullary) and extended through the inner longitudinal muscles into the cortical layer. This was interpreted at the time as being sufficient grounds to place it with the *Lytocestinae*. Recently the author has discovered two more genera, *Pseudolytocestus* and *Spartoides*, which possess this same arrangement of the vitellaria. These three genera are clearly alike in this important respect, and the author therefore placed them in a new subfamily, the *Pseudolytocestinae* (Hunter 1929). Attention has been called to the necessity of changing the subfamily designation from *Pseudolytocestinae* to *Capingentinae* since *Capingens* was picked as the type genus.\* There are now four subfamilies of the *Caryophyllaeidae*; the *Caryophyllaeinae*, *Capingentinae*, (= *Pseudolytocestinae*), *Lytocestinae* and *Wenyoninae*.

Phylogenetically the *Caryophyllaeidae* are undoubtedly closely allied to the bothriocephalid tapeworms. This is shown more clearly than ever by the new genera which were described by the author in 1927. Both the genus *Capingens* and *Biacetabulum* have type species whose scolices clearly resemble the bothria and acetabular types respectively. The morphological details of the musculature are likewise remarkably similar, an indication that the groups are closely allied. The final word, however, must be withheld until such time as the life histories of these parasites are worked out.

#### KEY TO THE GENERA OF THE CARYOPHYLLAEIDAE

- |   |                             |
|---|-----------------------------|
| 1 (37) <i>Caryophyllaeidae</i> with sexual apertures and ovary situated in last fourth of body length.....  | 2                           |
| 2 (18) <i>Vitellaria</i> entirely medullary.....  | <i>Caryophyllaeinae</i> 3   |
| 3 (12) <i>Caryophyllaeinae</i> with uterine coils extending anterior to the cirrus sac.....   | 4                           |
| 4 (10) Adults parasitic in fish.....  | 5                           |
| 5 (7) Ovary not "H" shaped.....   | 6                           |
| 6 Ovary shaped like inverted "A;" scolex undifferentiated; cirrus sac opens into utero-vaginal canal.....   | <i>Caryophyllaeides</i>     |
| 7 (5) Ovary "H" shaped.....   | 8                           |
| 8 (9) Scolex well defined, bearing one pair acetabular-like suckers; external seminal vesicle present.....  | <i>Biacetabulum</i> .       |
| 9 (8) Scolex poorly defined, bearing three pairs of loculi; cirrus opens on ventral surface or into a shallow atrium ahead of the female; external seminal vesicle present..... | <i>Hypocaryophyllaeus</i> . |
| 10 (4) Adults parasitic in body cavity of <i>Tubificidae</i> .....  | 11                          |
| 11 Caudal vesicle bearing embryonic hooks.....  | <i>Archigetes</i> .         |
| 12 (3) <i>Caryophyllaeinae</i> with coils of uterus never extending anterior to cirrus sac....  | 13                          |
| 13 (15) Scolex with terminal introvert.....   | 14                          |

\* Dr T. Harvey Johnston, The University, Adelaide, Australia kindly brought this matter to my attention.

14	Scolex hexagonal, with terminal introvert; 6 weak shallow grooves; cirrus and utero-vaginal canal open together in last fourth body length into a shallow evertible cloaca separated by bulky annular pad (male papilla?) . Monobothrium.	
15 (13)	Scolex without terminal introvert.....	16
16 (17)	Scolex with anterior extremity broadened or curled, not specialized into loculi, bothria, etc.; cirrus opens on ventral surface or into shallow non eversible atrium; no external seminal vesicle present.....	Caryophyllaeus.
17 (16)	Scolex well defined with 3 pairs of loculi or suckers; external seminal vesicle present.....	Glaridacris.
18 (2)	Vitellaria not entirely medullary, but entirely cortical or partly cortical.....	19
19 (31)	Vitellaria entirely cortical, lying external to the inner longitudinal muscle layer.....	Lytocestinae
20 (22)	Inner longitudinal muscle mass arranged in two parallel sheets between testes..	21
21	Lytocestinae with scolex possessing longitudinal loculi and distinct muscular "frill;" uterine coils do not extend anteriorly to cirrus sac and reach a maximum length of less than one-half that of testicular field.....	Balanotaenia.
22 (20)	Inner longitudinal muscles annularly arranged about testes.....	23
23 (26)	Scolex devoid of specialization.....	24
24 (25)	Lytocestinae with no post-ovarian vitellaria; uterine coils extend anterior to wings of ovary.....	Lytocestus.
25 (24)	Lytocestinae with vitellaria continuous laterally with post-ovarian group; uterine coils do not extend anterior to ovarian wings.....	Lytocestoides.
26 (23)	Scolex specialized (i.e. bears loculi, bothria, etc.).....	27
27 (29)	Uterine coils extend anteriorly nearly as far as testes.....	28
28	Lytocestinae with globular scolex armed with terminal sucker; uterine coils divide testicular field in half; post-ovarian vitellaria absent.....	Djombangia.
29 (27)	Uterine coils extend anteriorly less than one-half the length of testicular field..	30
30	Lytocestinae with scolex bearing longitudinal furrows and terminal introvert; uterine coils never extend beyond anterior wings of ovary; post-ovarian vitellaria absent.....	Monobothroides.
31 (19)	Vitellaria not entirely cortical, but having a medullary origin and extruding one third to one half (or more) into cortical parenchyma.....	Capingentinae (= Pseudolytocestinae)
32 (34)	Scolex occupying one-fifth or more of entire body length.....	33
33	Capingentinae with scolex bearing one pair of large bothroid suckers; post-ovarian vitellaria present.....	Capingens.
34 (32)	Scolex occupying less than one-fourth or one-fifth of body length.....	35
35 (36)	Capingentinae possessing "U" shaped ovary with cirrus sac lying within wings of ovary; external seminal vesicle present; no post-ovarian vitellaria present.....	Spartoides.
36 (35)	Capingentinae possessing undifferentiated scolex and "H" shaped ovary; no post-ovarian vitellaria; prominent external seminal vesicle..	Pseudolytocestus.
37 (1)	Caryophyllaeidae with sexual apertures in anterior half of body length.....	Wenyoninae
38	Longitudinal extent of uterus at least equal to that of testes; parasitic in Siluridae.....	Wenyonia



## FAMILY CARYOPHYLLAEIDAE LEUCKART 1878

Family diagnosis: Pseudophyllideans with or without organs of adhesion on scolex. Ovary and genital openings present singly, lying on ventral surface. Testes exclusively confined to medullary parenchyma; vas deferens located anteriorly to thick, muscular cirrus sac. Oviduct arises from oöcapt with origin in ovarian commissure. Utero-vaginal duct without sphincter. Two main longitudinal nerve strands are present.

## SUBFAMILY CARYOPHYLLAEINAE (Nybelin, 1922)

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated within last quarter of body length. Longitudinal muscles usually consist of two layers, inner always surrounding vitellaria which are medullary and typically annularly arranged. Uterine glands present.

Type genus: *Caryophyllaeus* Müller 1787.

## GENUS CARYOPHYLLAEUS O. F. MÜLLER 1787

Generic diagnosis: Caryophyllaeinae with broadened, folded or "curled" anterior extremity not specialized into loculi, bothria or suckers. Cirrus opens on ventral surface or into shallow non-eversible genital atrium. Medullary ovary "H" shaped. Uterine coils never extend anterior to cirrus sac, with maximum length one-third that of testicular field, usually less. No external seminal vesicle; post-ovarian vitellaria and terminal excretory bladder present. Parasitic in digestive tract of Cyprinidae and Catostomidae. Development unknown; procercoid stage supposed to occur in body cavity of Tubificidae.

Type species: *Caryophyllaeus laticeps* (Pallas 1781). To include:

- (1) *C. laticeps* (Pallas 1781) (= *C. mutabilis* Rud. 1802)
- (2) *C. syrdarjensis* Skrjabin 1913
- (3) *C. armeniacus* Cholodkowsky 1915
- (4) *C. caspicus* Klopina 1919
- (5) *C. fimbriceps* Klopina 1919
- (6) *C. terebrans* (Linton 1893)
- (7) *C. gotoi* Motomura 1927
- (8) *C. javanicus* Bovien 1926
- (9) *C. oxycephalus* Bovien 1926
- (10) *C. serialis* Bovien 1926
- (11) *C. tenuicollis* Bovien 1926
- (12) *C. microcephalus* Bovien 1926
- (13) *C. acutus* Bovien 1926

It is very probable that the six species described by Bovien (1926) will be placed in other genera after further study. Bovien realized this when he said "No doubt the genus *Caryophyllaeus* in the rather wide sense

adopted in my paper shall have to be divided, but considering the rapid increase in the number of species, I prefer to wait." These six species are all found in members of the Siluridae which is one of the characteristics of the Lytocestinae. Furthermore, none of Bovien's species possess post-ovarian vitellaria which is more typical of the Lytocestinae than the Caryophyllaeinae. It is, of course, impossible to determine their true position without further study, as there are no figures of sectioned material.

*CARYOPHYLLAEUS TEREBRANS* (LINTON 1893) Char. emend.

[Figs. 1, 30, 31, 51, 72]

1893: <i>Monobothrium terebrans</i>	Linton	1893: 545-564
1922: " <i>Monobothrium</i> " <i>terebrans</i>	Nybelin	1922: 123-124
1923: <i>Caryophyllaeus terebrans</i>	Woodland	1923: 450-460
1927: <i>Caryophyllaeus terebrans</i>	Hunter	1927: 18

Specific diagnosis: With characters of genus. Adult parasites measuring 5 to 30 mm. in length and 0.8 to 2.5 mm. in width frequently embedded in the intestinal wall. Neck distinct, slightly narrower than dorso-ventrally flattened body. Cuticula 5 to 10  $\mu$  thick; subcuticula 6 to 15  $\mu$  thick, followed by cortical parenchyma 50 to 75  $\mu$  in depth. Inner and outer longitudinal muscles present and equally prominent. Testes nearly spherical, numbering 175 to 225 in normal adults, with maximum diameter from 0.15 to 0.27 mm. Ovoid to round cirrus sac occupies one-third to one-half of medullary parenchyma; diameter varying between 0.2 and 0.45 mm.; circular muscles from 12 to 19  $\mu$  in thickness. Inner band of circular muscles forms inner cirrus sac varying between 0.2 and 0.27 mm. Male and female reproductive systems open on surface 0.09 to 0.2 mm. apart. Vagina median, ventral, convoluted, not forming receptaculum seminis. Length of ovarian wing, varies between 0.6 and 1.15 mm. by 0.13 to 0.3 mm. Maximum diameter of vitellaria 0.228 mm. Eggs ovoid 55 to 65 by 30 to 36  $\mu$ .

Host: *Catostomus ardens*, Heart Lake, Yellowstone National Park, Wyoming; *Ictiobus bubalus*, Tallahatchie River, Money, Mississippi. In intestine.

Paratype: Linton's original slides, two in number (233/1) loaned to Prof. H. B. Ward, University of Illinois, Urbana, Illinois.

Bottled material in author's collection No. 645.

Host	Locality	Collector	Authority
<i>Catostomus ardens</i> Jordan and Gilbert	Heart Lake, Yellow- stone Nat'l. Pk., Wyo.	E. Linton	Linton 1893: 545-564
<i>Ictiobus bubalus</i> (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)



This species has the distinction of being the first Cestodarian parasite to be recorded from North America. Dr. Edwin Linton secured the material from the intestine of *Catostomus ardens*. The fish were taken on July 28, 1890 by a trammel net in Heart Lake, Yellowstone National Park. The revised description of this species is based upon the original paper of Linton (1893), upon some of his original slides and some of the same species collected from *Ictiobus bubalus* in the spring of 1927 by Dr. Parke H. Simer near Money, Mississippi.

The original description was based largely upon contracted forms. One of the slides loaned to Professor Henry B. Ward was a sexually mature specimen measuring but 5 mm. long whereas no mature forms collected by Dr. Simer were under 20 mm. in length. The minimum measurements therefore will be based upon Dr. Linton's slides and the maximum upon the normally contracted forms in the author's collection.

The parasites range between 5 and 30 mm. in length. Sexually mature parasites appeared from 20 mm. and up in cases of normal contraction. The scolex typically is bluntly rounded or cone shaped, and tapers into a neck, the narrowest part of the body (Fig. 1). In cross section the neck is round although posteriorly the body is oval. *C. terebrans* is much wider proportionately than any other parasite described. It possesses a width of 0.8 to 2.5 mm. The latter figure is cited by Linton as the breadth of a specimen 17 mm. long. In highly contracted forms the maximum width occurs at the base of the scolex just before it passes into the neck.

The parasites were not found originally in any considerable numbers; only twelve being taken from two fish. Some were embedded in the intestinal wall in pits, frequently several being found in the same cavity. One specimen was described by Linton (1893: 548) as follows: "Upon examining the alocholic specimens one was found 7 mm. in length, which was wholly inclosed in a pit in the mucous membrane. The walls of the pit were thick and gristly and the head end of the parasite had nearly perforated the intestinal wall." None of the specimens secured from Mississippi showed this characteristic.

The scolex of this species is perfectly smooth and bears no suckers or loculi. The slides as well as the original description substantiate this. The general shape of the head, as described by Linton is "variable, subsagittate, wedge shaped or bluntly rounded, a little broadened and thicker than the body, somewhat depressed dorso-ventrally—." A frontal section of the scolex shows the presence of a great number of longitudinal muscle fibers from the inner longitudinal system. All of these fibers extend to the distal portion of the scolex where they disappear in the subcuticula and basement membrane. It is evident, as in other forms, that these muscle fibers are inserted on the latter structure. The outer longitudinal muscles as reported by Linton (1893:550) do not show in sagittal sections but are

very evident in material from the author's collection which has been cross sectioned (Fig. 72). Cross muscle fibers are found in considerable numbers in the scolex; these extend both in a lateral as well as a dorso-ventral plane.

The entire scolex is composed of a spongy matrix of parenchymatous tissue. Here are found the canals of the excretory system. The canaliculi of the ascending system were traced in considerable numbers to the distal parts of the scolex. It is probable that these canals aid in the elongation of the scolex. It is easy to conceive that the fluids of the excretory system if forced to the anterior end would fill the canals and canaliculi and thereby cause the protrusion of the scolex. Such an extension could not occur without the aid of some of the muscles of that region, the presence of the cross fibers of the scolex suggesting that such fibers prevent the lateral expansion of the scolex and thereby aid in the anterior extension of the scolex. Retraction of the scolex is readily accomplished by the contraction of the large inner longitudinal muscles.

There is one other peculiarity of this scolex. Here, as in the case of *Monobothrium ingens*, the posterior central portions of the scolex contain numerous bodies staining readily with eosin. In the latter case, however, these bodies are confined laterally by the inner longitudinal muscles and in the former are restricted only to the cortical and medullary parenchymal regions; in the material of *C. terebrans* at hand the two are inseparable. These bodies are nucleate and filled with globules and are irregular in shape. It was impossible to definitely trace them to the excretory system and so far it has been equally impossible to connect them with any other organ system. They may be excretory products secreted through the activity of the scolex which are later to be dissolved, resorbed and carried off by the excretory system. Or, they may be glandular cells concerned with the penetration of the parasite through the mucosa of the intestines.

The integument is composed of the cuticula, basement membrane and the cuticular muscles, circular and longitudinal. In Linton's specimens the cuticula is very thick, measuring 10 to 16  $\mu$ , the lower 0.8 to 1  $\mu$  being distinguishable as the basement membrane. In older specimens the cuticula is vacuolated reminding one of the descriptions of the foramina secundaria noted by Fraipont (1881), except that they do not open to the outside. These vacuoles usually circular are irregular in shape, the largest measure 3 $\mu$  in length. They lie in the middle of the cuticula which appears smooth on the outer surface and is bounded medianly by the basement membrane. Within these two smooth areas lies the vacuolated portion of the cuticula. The granules appear to be situated in a reticulum composed of fine canaliculi. This may have been caused by poor fixation or possibly by a partial breakdown of the cuticula. In the material collected in 1927 the

cuticula varied between 5 and  $7\mu$  in thickness and showed no such characteristics.

The cuticular muscles are beneath the basement membrane. The outer circular muscles are less than  $0.8\mu$  in thickness. The longitudinal cuticular muscles, on the other hand, are nearly twice as thick, measuring from 1 to  $3\mu$ . These two sets of muscles are situated at the outermost edge of the dense nucleate layer of the subcuticula. This layer extends medianly to the outer longitudinal muscle band 15 to  $33\mu$  from the edge of the cuticula. These muscles mark the end of the subcuticula and separate it from the cortical parenchyma. Normally most of the subcuticular cells are found within the confines of the subcuticula. In this species, however, the cortical parenchyma is just about as densely packed with parenchymal cells as is the subcuticular layer. The presence of the canals of the excretory system in the cortical parenchyma is the one character which distinguishes the two. The reproductive organs nearly fill the medullary parenchyma with its scattered parenchymal cells.

The muscular system, as in other members of the Caryophyllaeinae, is divided into two portions, the cuticular and the parenchymal. The former has been described in detail in the preceding paragraphs and will not be reconsidered. The parenchymal muscle system appeared well developed in one of Linton's slides. It extends into the posterior third of the body as a distinct layer whose position varies between 15 to  $33\mu$  from the exterior. This great range is caused by the outer longitudinal muscles being pushed outward, as the uterus becomes distended with eggs. These muscles extend anteriorly into the scolex and pass to the mid-lateral region where they become attached.

The inner longitudinal muscles lie 60 to  $95\mu$  from the outer edge of the cuticula and extend from the posterior tip to the distal end of the scolex where the fibers break up to become inserted in the basement membrane. After the neck is passed these fibers arrange themselves as a definite sheath about the vitellaria which in turn nearly surround the testes (Fig. 72). The fibers of this muscle layer extend to the posterior tip of the body where they are not inserted on the basement membrane, but form a continuous sheath about the post-ovarian vitellaria. The continuity of these fibers is broken ventrally by the cirrus sac. A few are inserted posteriorly on the excretory bladder. One of the slides studied was a frontal section of an adult which had contracted to 5 mm. in length. In this specimen the inner longitudinal muscles assumed their natural position just as the anterior testes were reached 1.2 mm. from the distal tip of the scolex.

The dorso-ventral as well as the lateral muscle fibers are abundant, especially in the medullary parenchyma; the diagonal muscle fibers, however, are limited. Specialized muscles appear in the scolex where the longitudinal layer of cuticular muscles become converted into the small transverse



fibers which permeate this region. It is probable that their origin is the same as those described for *Biacetabulum infrequens*, *Capingens singularis*, etc. Other specialized muscles will be described in connection with the systems in which they occur.

The major portions of the excretory system are found between the inner and the outer bands of longitudinal muscles. These paired canals extend from the anterior portions of the scolex where they are found scattered throughout the cortical and medullary parenchyma to the posterior extremity. At this point they empty into the excretory vesicle described by Linton (1893: 550) as follows:

"A terminal pore leading into a short duct with thick walls was observed in transverse sections through the posterior end of a small specimen. The duct enters posteriorly from near one margin and not from the extreme tip, and continues anteriorly to the posterior vitelline gland. The same was observed in transverse sections of larger specimens, where it appeared first in the posterior sections as a pore entering one of the margins, and was soon seen, in succeeding anterior sections, toward the middle of the sections as an elongated opening with strong walls of connective tissue of irregular thickness. In the smaller specimens strong connective fibers run from the anterior end of this cul-de-sac. This organ is doubtless the terminal pulsating organ common to larval cestodes."

This description is adequate. Ten pairs of main excretory canals were present, although their number was increased in the anterior end where they broke up into numerous canaliculi of the ascending system (Fig. 72). These extend to the distal portion of the scolex. As has already been described in the paragraphs dealing with the scolex these canaliculi when filled with the products of the excretory system become turgid and aided by the transverse muscle fibers, cause the elongation of the scolex. This is in accord with the phenomena observed in living specimens of other species.

The testes are found within the inner longitudinal muscle layer almost completely surrounded by the vitellaria. In young specimens the testes begin about the anterior third or fourth of the body. Actual count of the number of testes in Linton's specimen was 81. The other slide loaned by him, a section of the posterior region, indicated the presence of considerably more. A check made upon the material secured in 1927 indicates a close correlation with the original except in the matter of the testes count. This was found to be between 175 and 225. The arrangement and size of all structures are essentially identical in the slide of the posterior region and my own material, clearly pointing to the identity of the forms. The only apparent explanation is two fold, either Linton had representatives of two species or that one matured unusually early before the male reproductive system had completed its development, the reverse of the normal con-

dition. The latter explanation has been accepted by the author. The true testes count based upon a study of three sexually mature adults clearly places the number between 175 and 225. In sections they appear irregularly ovoid in shape, ranging between 0.13 to 0.27 mm. long and 0.09 to 0.16 mm. wide (Fig. 72).

No connection could be demonstrated between the vas deferens and the testes which lie in a dorsal and ventral row between the lateral rows of the vitellaria. These have the appearance of surrounding the testes for they are intermingled between them in all except the lateral region. The usual arrangement is an alternation of testes and vitellaria (Fig. 72). As in the case of the other species studied the vas deferens lies close to the testes and even appears to bend towards first one and then another testis. The vas deferens descends posteriorly from a median position and enters the portion of the medullary parenchyma anterior to the cirrus sac. This region is devoid of testes and vitellaria. The vas deferens is thin-walled and passes ventrally into a convoluted region between 0.15 and 0.67 mm. in length. The entire region occupied by the vas deferens is triangular with the base against the anterior side of the cirrus sac. It is swollen and filled with spermatozoa. The maximum diameter of the expanded tube varies between 84 and 120  $\mu$ . The convolutions of the vas deferens pass dorsally and enter the muscular ductus ejaculatorius the diameter of which is between 30 and 54  $\mu$ . The lining of this tube is characteristic of the seminal vesicle and the cirrus sac. The thin walls of the vas deferens are supplanted by a thicker membrane which in turn is surrounded by a wall of circular muscles 18 to 28  $\mu$  in thickness. The ductus ejaculatorius does not form a characteristic seminal vesicle; Linton in his original description neither mentions this, nor figures it, and the slides at my disposal do not show the presence of a true external seminal vesicle. Neither is the distal portion of the cirrus sac modified to form an internal seminal vesicle. The ductus ejaculatorius is convoluted, extending to the anterior median, lateral wall of the cirrus sac where it becomes surrounded by some of the muscles of the cirrus sac. It extends to the dorsal surface where it penetrates the remaining layers of the muscles to the innermost portions of the cirrus sac proper (Fig. 30, 31).

The circular cirrus sac is penetrated from the dorsal surface, slightly posterior to the center (Figs. 30, 51). As the cirrus itself is retracted, the tubules of the sac are closely coiled in the dorsal portion. The cirrus sac occupies about one third to one half of the medullary parenchyma and measures 0.2 to 0.45 mm. in greatest diameter. There appear to be two layers of circular muscles which compose the cirrus sac as a whole. The inner circle of muscles which varies between 0.2 and 0.27 mm. surrounds the cirrus sac proper. This checks with Linton's original material which measures 0.14 to 0.2 mm. The circular muscles of the outer and inner



regions of the cirrus sac are 25 to 31  $\mu$  and 8 to 15  $\mu$  respectively. The outer layer functions in the retraction of the cirrus. Linton (1893: 551) reports finding all the cirri retracted. The cirrus aperture, as seen in section is irregular and shows "puckered walls." The long axis of this aperture lies transversely to the long axis of the body. (Fig. 30.)

The vitellaria are described by Linton (1893:551) as consisting of "two marginal glands which connect with a posterior gland lying behind the ovary. In the adult specimens this organ may be divided into at least three distinct glands, one posterior and two marginal." These observations coincide with my material with but one exception. The irregularly rectangular vitellaria extend as a band and nearly surround the testes. They pass laterally and posteriorly as far as the cirrus sac. In sections their measurements vary between 0.05 and 0.22 mm. in length and 0.016 to 0.076 mm. in width. Linton (1893:551) describes the vitelline ducts as sometimes being crowded with small globular masses. This condition is typical of vitelline ducts. He neglects to mention the number and distribution of these ducts, other than note that they connect with the oviduct near the dorsal posterior edge of the ovarian commissure (germ gland). Linton's figures indicate the presence of 6 vitelline ducts, three from each side. The anterior one comes from the marginal anterior vitelline glands and unites with the oviduct (germ duct). According to Linton's figures the combined ducts pass posteriorly where they are joined from the sides by the other two vitelline ducts from the post-ovarian vitellaria. These in turn are supposedly composed of two ducts, one from the median portion of the post-ovarian vitellaria and one from the lateral. My material, however, shows clearly the presence of single vitelline ducts uniting with the oviduct. The anterior vitelline ducts first appear median to the outer row of the vitellaria and anterior to the vas deferens and the uterus. This canal passes laterally to a position just within the inner longitudinal muscles and between them and the expanded uterine coils. As the ovary is reached the vitelline ducts again turn medianly and slightly ventrally so as to pass beneath and on the inside of the main ovarian wings. As the ovarian commissure is passed the vitelline ducts pass medianly and are joined by similar canals which originate from the most anterior portion of the post-ovarian vitellaria. This common vitelline duct continues medianly along the posterior edge of the commissure until nearly in the center of the parasite. It then turns posteriorly, to the right, and sometimes expands to form a vitelline reservoir. The oötype lies close beside it and the vaginal-oviducal canal (fertilization chamber) is joined by this common vitelline duct before the center of the oötype is reached (Fig. 51).

Globular lobate ovary is situated near the ventral surface and possesses the characteristic "H" shape. Its length measures between 0.6

and 1.15 mm. and the width varies between 0.13 and 0.30 mm. The ovarian commissure the median portion of which serves as an ovarian reservoir has a maximum diameter of 0.3 mm. The wings of the ovary extend posteriorly to the vitelline mass at the posterior tip of the body, and anteriorly until they reach the uterine coils. Linton (1893:551) reports the degeneration of the ovarian commissure when the uterus is filled with developing embryos. None of the material studied by the writer showed this characteristic.

The oöcapt arises from the ovarian commissure on the median posterior side. The sphincter muscle controlling the release of eggs is small, as is the canal. The oviduct takes its origin from the distal end of the oöcapt which is situated on the posterior edge of the ovarian commissure. The tube is 4 to 6  $\mu$  in diameter and is surrounded by a layer of cells which surrounds the cuticula-like lining and in its turn is covered by a layer of circular muscles 7 to 9  $\mu$  thick. The total diameter of the tube, including the lining cells, is 27 to 33  $\mu$ . The oviduct passes posteriorly for 50 to 75  $\mu$  where it is joined by the vagina. This duct arises anteriorly from the posterior margin of the female utero-vaginal canal cloaca, passes posteriorly near to the middle of the body. The course of the vagina is rather tortuous for it is pushed this way and that by the distended, egg-filled uterus. As the ovarian commissure is approached the vagina swings dorsally and passes over it, then drops ventrally and unites with the oviduct. It was not possible to demonstrate a receptaculum seminis such as Linton (1893:552) described. The width of the vagina is nearly constant having a diameter of 36 to 40  $\mu$ . The walls are surrounded by a thin layer of circular muscles.

As already described, the vagina meets the oviduct 50 to 75  $\mu$  from the origin of the latter. This combined oviducal-vaginal canal (fertilization chamber) passes posteriorly and towards the right side where it enters the oötype complex. The vitelline ducts which have now united in a single duct, and have become swollen and convoluted, functioning as a reservoir, join the combined vaginal-oviducal canal to form the beginning of the uterus. The uterus passes through several convolutions within the oötype. It then winds posteriorly into the thin walled portion which lies between the ovarian commissure and the post-ovarian vitellaria. The uterine canal proceeds dorsally and medianly, passes anteriorly over the ovarian commissure and between the wings of the ovary. This convoluted canal continues, never passing anterior to the cirrus sac, until it finally dips ventrally and empties to the ventral surface 0.09 to 0.2 mm. behind the cirrus sac. The vagina empties into this common female cloaca from the posterior side as already described (Fig. 30). The pores of the male and female systems are therefore separated and do not open into a common genital atrium, but lie 0.09 to 0.2 mm. from each other.

The eggs of this species were nearly all contracted out of shape so that accurate measurements were difficult to secure. They are ovoid and as far as it was possible to determine, non-operculate. The size ranges between 58 and 65  $\mu$  in length and 29 to 35  $\mu$  in breadth. This essentially substantiates the measurements given by Linton. The shell is 1.5 to 2.1  $\mu$  in thickness. The globular masses within the shell are about 10.5  $\mu$  in diameter.

*C. terebrans* was recorded originally from *Catostomus ardens*, but has since been found in *I. bubalus*.

The lack of specialization of the scolex coupled with the absence of an external seminal vesicle places this form in the genus *Caryophyllaeus*. *C. terebrans* was the first Cestodarian to be recorded from this continent; it also was the first record of this group of parasites from fish of the family Catostomidae. There are three other species of the Caryophyllaeidae which are known to occur in the same genus, *Catostomus*. The dearth of suckers or loculi distinguishes *C. terebrans* from all the members of the genus except *C. laticeps*, *C. syrdarjensis*, *C. armeniacus* and *C. gotoi*. The first two and the last possess scolices which are broader at the apex and not conical as in *C. terebrans*. *C. syrdarjensis* is further demarked by the presence of four longitudinal rows of "Fäserzellenstränge" and in shape and position of the cirrus sac. *C. gotoi* recorded by Motomura (1927) appears to have been inadequately described. It differs from *C. terebrans* in body length, shape of the scolex, number of testes (being only 30 to 40) and the presence of a receptaculum seminis. In addition it is recorded from a new host, *Misgurnus anguillicaudatus*. *C. laticeps* also differs from *C. terebrans* in the number of testes, 350 to 400, which was checked by Nybelin's (1922:126) count of 366. This difference coupled with the presence of a receptaculum seminis, type, angle, and size of the cirrus sac, length of the female genital atrium, and length of the ovary, clearly separates *C. laticeps* from *C. terebrans*. The description of *C. armeniacus* is inadequate, but the greater length and breadth, 55 mm. and 5 mm. respectively, the absence of post-ovarian vitellaria and the immense eggs eliminates the possibility of *C. armeniacus* being a synonym of *C. terebrans*. The two species described by Klopina (1919), *C. caspicus* and *C. fimbriceps* differ from *C. terebrans* in the type of scolex which is broadened and "curled" in both cases and also both her species are characterized by rows of "Fäserzellenstränge" which are not found in the latter. *C. terebrans* differs from the six species described by Bovien (1926) in the host and in the possession of post-ovarian vitellaria. One other difference should be noted, all of the Caryophyllaeidae found thus far on the North American continent are found in members of the Catostomidae, see Essex and Hunter (1926), whereas those from Europe are typically found in the Cyprinidae. *C. terebrans* is readily distinguished



from all the species thus far described on this continent and is the only species recorded for the genus *Caryophyllaeus*.

#### GENUS MONOBOTHRUM DIESING 1853.

Generic diagnosis: *Caryophyllaeinae* with scolex round to oval in cross section, bearing 6 shallow longitudinal grooves and terminal funnel-shaped introvert. Cirrus and utero-vaginal canal open together into a shallow, eversible, common genital atrium, widely separated by bulky annular pad (male genital papilla?). Ovary "H" shaped, entirely medullary. Uterine coils never anterior to cirrus sac, with maximum length one third that of testicular field, usually less. External seminal vesicle and terminal excretory bladder present. Post-ovarian vitellaria may or may not be present. Parasitic in digestive tract of Cyprinidae and Catostomidae. Development unknown.

Type species: *Monobothrium wagneri* [= *M. tuba* (v. Siebold 1853)] Nybelin 1922.

To include:

- (1) *M. wagneri* Nybelin 1922
- (2) *M. ingens* Hunter 1927

The author feels that in the light of the previous discussion this genus should be retained as valid. One of the criteria of usefulness is whether or not other new forms will fit into it. In 1927 the author published an account of a species which clearly and distinctly fell into the confines of this genus. The genus therefore has earned itself a permanent place in the classification of the *Caryophyllaeidae*.

#### MONOBOTHRUM INGENS HUNTER 1927

[Figs. 8, 9, 29, 39, 79-83]

1927: *Monobothrium ingens*

Hunter 1927:19

Specific diagnosis: With characters of genus. Adult parasites embedded in pits in mucosa of intestine. Length, 45 to 75 mm.; width, 0.9 to 1.2 mm. Neck distinct, 4 to 5 mm. long, 0.69 mm. maximum width. Longest longitudinal grooves on dorsal and ventral surfaces. Body broadens posteriorly, oval in cross section. Cuticula 5 to 6  $\mu$  thick; subcuticula 10 to 15  $\mu$  deep, bounded medianly by cortical layer of parenchyma which is 20 to 40  $\mu$  thick. Both inner and outer longitudinal muscle layers well developed and prominent. Testes 300 to 325, roughly ellipsoidal with maximum diameter of 0.192 to 0.298 mm. Cirrus sac lies at an angle of 45 degrees with horizontal, oval occupying about one half of medullary parenchyma; maximum diameter 0.35 mm.; circular muscles 12 to 36  $\mu$  thick. Female genital atrium opens into eversible cloaca, 0.19 mm. posterior to the male orifice. Vagina straight, not forming recep-

taculum seminis. Wings of ovary 0.8 to 1 mm. long; ovarian commissure 0.19 to 0.3 mm. in diameter. Vitellaria have maximum diameter of 0.18 mm. Post-ovarian vitellaria absent. Excretory system characterized by 10 pairs of main canals. Eggs 53 to 58 by 28 to 33 $\mu$ .

Host: *Ictiobus cyprinella*, Lake Pepin, Minnesota. In intestine.

Type: Slides No. 29.40 in the collection of Dr. Henry B. Ward.

Paratype: Alcoholic specimens and slides in the author's collection Nos. 427, 428.

Host	Locality	Collector	Authority
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

*Monobothrium ingens* was parasitic in the intestine of *Ictiobus cyprinella* (large mouth buffalo). These worms were found with their scolices affixed in pits in the mucosa and submucosa. These pits were deep and also showed considerable proliferation of tissue, so that they protruded into the intestinal cavity. The size of the cysts was nearly uniform. The largest measured 17 by 14 mm. by 12 mm. in depth. Usually more than one parasite was found in a pit; the greatest number was 7.

The parasites themselves proved to be some of the largest of the Caryophyllaeinae, for when alive and in an extended condition they measured 65 to 75 mm.; this was not materially altered by fixing reagents. These parasites present a distinctly uniform exterior, as they were flattened dorso-ventrally, with the exception of the neck and scolex which is more rounded than the other body regions. The cuticula is thick and gives a striated appearance to the surface of the worm.

The region of the scolex, although showing but little differentiation, is clearly marked off from the rest of the worm. It is about 2 mm. in length by 0.9 mm. in width and bears upon the dorsal and ventral surfaces two shallow and poorly defined loculi (Fig. 8). There are four others present, but these are more clearly visible in cross sections. Behind the scolex is a distinct neck, measuring approximately 0.69 mm. in width. This region is filled with a mass of excretory tubules which are visible in the toto mounts. The distance from the base of the scolex to the first of the vitellaria is variable due to the degree of contraction, but is between 4 and 5 mm. Posteriorly the body becomes broader reaching a maximum width of 0.9 to 1.2 mm. The body then tapers posteriorly until the region of the female reproductive system, just posterior to the cirrus sac,



is reached; here it has a maximum width of 1.11 mm. Unlike most of the Caryophyllaeinae the female reproductive system with the exception of the vitellaria is confined to the last twelfth of the body length.

The scolex of *M. ingens* places it clearly in the genus *Monobothrium*. It possesses a characteristic hexagonal scolex, each depression being a small loculus while at the anterior extremity is an eversible introvert (Figs. 8, 9). This fact may explain why the worms were uniformly found in pits in the musoca. The use of this organ is apparent if the living material is studied, for it was this portion of the parasite which was extruded for a considerable length and then retracted suddenly. The introvert may be turned in for a distance varying between 30 and 45  $\mu$  (Fig. 9).

In the study of sections no dark staining bodies appear for the first 50  $\mu$ . At this point, however, in a normally contracted specimen, the parenchymal cells as well as the tubes of the excretory system first appear. These tubes and tubules are confined to the region of the cortical parenchyma. This layer is bounded on the one hand by the outer longitudinal muscle bands and on the other by the large inner longitudinal muscles. About 0.3 mm. from the inner end of the introvert cross sections show cross muscle fibers dominating the region; these run at right angles to one another. The greater portion of them are inserted in the basement membrane of the scolex, although some of them may be seen attaching themselves to the fasciculi of the inner longitudinal muscle bands, while a few disappear into the parenchymal mass. The insertions, in the case of the dorso-ventral fibers, are in the region of the middle loculus; the lateral muscles are inserted on the median lateral surface of the parasite. In the center where these fibers cross at right angles are a number of deep staining parenchymal cells. These muscle fibers are found for a short distance only and are apparently highly specialized muscles. By contracting, they would cause a decrease in the breadth of the scolex thus aiding in the extension of the scolex. The neck region and posterior parts are incapable of much change, and it is known from observations on living material that the scolex is capable of considerable expansion. Thus it would seem that the contraction of these muscles at the base of the scolex would cause the elongation of this organ and the eversion of the introvert (Fig. 9).

The six loculi characteristic of the genus *Monobothrium* appear 0.11 mm. from the anterior extremity of the scolex and gradually disappear, except for the median ones on the dorsal and ventral surfaces, which run posteriorly for nearly one-third of the body length. These loculi are poorly defined and show little or no specialization. The only indication in this region is a slight thickening of the cuticula and cuticular muscles.

The cuticula of this Cestodarian parasite is composed of several layers.

The outermost portion is thin, being nearly  $1\ \mu$  thick and stains readily with eosin. Under this lies the cuticula proper which has a thickness of  $4\ \mu$  or more including the basement membrane. This latter structure measures nearly  $1\ \mu$  across. These three layers, collectively known as the cuticula, are between  $5$  and  $6\ \mu$  in width. There is little or no change in the thickness of these integumental layers in the different portions of the body, with the exception of the scolex where all three become slightly thicker. As is the case of all of the Caryophyllaeinae there are two layers of cuticular muscles which underlie the basement membrane. This muscle system is comprised of an outer layer of circular muscles,  $1\ \mu$  in thickness, situated just beneath the basement membrane, followed by the longitudinal muscle layer of the cuticula which is slightly more prominent, being about  $4\ \mu$  wide, and lying medianly to the circular muscles. The muscles just described are embedded in that portion called the subcuticula. This will be described in the paragraphs which follow.

The parenchyma of this parasite is divided into three portions, the outermost or subcuticula, the cortical and medullary parenchyma. The subcuticula extends  $10$  to  $15\ \mu$  medianly from the basement membrane. In it are embodied the circular and longitudinal muscles of the cuticula, and a profusion of parenchymal cells. These cells form an irregular row lying between the longitudinal cuticular muscles on the one hand and the outer longitudinal muscle bands of the parenchymatous system on the other. These oval cells are characteristic, and stain deeply with hematoxylin; the nucleus and cytoplasmic bodies standing out with great clearness. Each cell is embedded in a mass of fibers which extend towards the basement membrane and roughly parallel one another. At the median border of the subcuticula is found the outer longitudinal muscle layer of the parenchymal system. These muscles are grouped  $3$  to  $9$  together in a fasciculus (Fig. 81). In the scolex the number of fasciculi are reduced and the fibers increase to  $10$  or  $14$  per fasciculus. The cortical layer of the parenchyma lies between the outer and inner longitudinal muscle bands. The parenchyma is less dense here and the cells are fewer in number. This is the region in which are found the paired longitudinal canals of the excretory system, the ascending canal being the more median.

The medullary parenchyma contains the reproductive systems, which in turn are surrounded by the inner longitudinal muscles. The fasciculi containing these muscle fibers are about  $19$  to  $48\ \mu$  in width and lie  $20$  to  $40\ \mu$  within the outer longitudinal muscles. In this layer the mass of parenchymal cells is greatly reduced due to the excessive specialization of the reproductive systems. Occasionally dorso-ventral and lateral muscle fibers are found. The former are more profuse, and extend across the medullary parenchyma, passing between the inner longitudinal muscles and frequently giving off fibers to them. Eventually these fibers reach

the subcuticula. Here they split and disappear into the base of the subcuticula where they are apparently inserted on the basement membrane (Fig. 81).

The musculature is similar to that of other closely related species of the Caryophyllaeinae and is composed of two distinct sets of muscles which are found in different parts of the body. The cuticular muscles have already been described in the portion dealing with the cuticula.

The parenchymatous muscle system is the most prominent one found in the body. It is composed of two sets of longitudinal muscle fibers and a set of sagittal (dorso-ventral) and frontal (transverse) muscle fibers. This system of muscles controls the action of the scolex to a large extent, although dealing primarily with its contraction. The longitudinal muscle system is composed of outer and inner longitudinal muscle layers, the former lies at the base of the subcuticula and separates it from the cortical parenchyma. In mature specimens these muscles appear to be in cavities in the parenchyma. This is the smaller of the longitudinal sets and each fasciculus is composed of only 6 to 9 individual fibers (Fig. 81). The muscles are 14 to 21  $\mu$  from the outer edge of the cuticula in the posterior portion of the body as compared with 24 to 28  $\mu$  in the middle part. This difference occurs, however, only in cases of the parasites whose uteri are distended by eggs. As the anterior portion of the body is reached the outer longitudinal muscles break up and disappear into the scolex. The inner longitudinal muscle mass is by far the most prominent one in this species. It extends from the anterior part of the scolex to the posterior extremity of the body. These as well as the outer longitudinal muscles are broken ventrally by the presence of the cirrus sac. The inner longitudinal muscles in the posterior tip are 96 to 108  $\mu$  from the outside. They help to keep the reproductive organs in position, as the testes and vitellaria tend to extend past these muscles and into the cortical parenchyma.

As the scolex is approached the subcuticular layer grows deeper and the longitudinal muscles of the cuticula are more distinct. Slightly more anteriorly some of the inner fibers turn medianly and pass to the opposite side. On the ventral surface some turn and swing dorsally up and across to the dorsal side. This region of the base of the scolex is filled with many excretory tubules while in the medullary parenchyma a mass of unusual gland-like bodies appear, the exact function of which is uncertain. Branches from the inner longitudinal muscle mass, however, frequently penetrate to these cells. The inner muscles, contrary to the condition in some Caryophyllaeinae, especially *Glavidacris catostomi* Cooper (1920), do not divide into 8 large fasciculi in the neck, but retain the ring shaped formation. The bundles also increase somewhat in size in this region.

In cross and sagittal sections the dorso-ventral (sagittal) and lateral



(frontal) muscle fibers appear and may be traced. These are first found indistinctly in the lower portion of the scolex but from the neck posteriorly they increase in number and thickness. This is particularly noticeable in the case of the dorso-ventral fibers.

There are also certain specialized muscles which are found in various parts of the body. The first to be mentioned are the cross fibers found in the base of the scolex. These extend dorso-ventrally and laterally and aid in the elongation of the scolex. Their insertions lie in the basement membrane and the inner longitudinal muscles. The seminal vesicle is distinctly muscular, being surrounded with circular muscles. This condition pertains also in the ductus ejaculatorius, and in the cirrus sac to a less marked degree. The lower end of the uterus is also surrounded with circular muscles for a distance of 150 to 200  $\mu$ , and there is the sphincter muscle of the oöcapt between the ovarian reservoir of the commissure and the beginning of the oviduct. This completes the specialized musculature of *M. ingens*.

Little can be seen of the excretory system in toto mounts except a few longitudinal canals running throughout the body length. A close study of the anterior region, however, reveals the presence of a mass of tubules. In cross section this is very evident, the neck region and base of the scolex being filled with a mass of cross canals and smaller canaliculi. These tubules are difficult to trace, but it is apparent that they are confined to the region between the outer and inner longitudinal muscles. Ten pairs of main longitudinal canals in the neck region are so arranged that there are four ventral, four dorsal, and two lateral pairs of canals. Each pair is comprised of a large descending and a smaller ascending canal lying medianly to the descending one. These extend posteriorly and are connected by numerous cross passages. In all cases the smaller ones parallel the main descending canals. Finally in the region of the female reproductive system the small ascending canals are composed of smaller canaliculi originating in terminal excretory cells. These may be modified flame cells (Fig. 80). They appear at the ends of small tubules which are the beginnings of the ascending canals. The cell caps the tubule like a typical flame cell; it is 5 to 6  $\mu$  broad and does not appear very dissimilar from a typical parenchymal cell, thereby suggesting a common origin. The cells stain less deeply with hematoxylin than the parenchymal cells. Dark radiating strands are seen extending into the protoplasm of the cell. On the inner surface, projecting out into the tubule can be seen the cilia of the excretory cell. This flame cell is smaller than the "renal corpuscle" described by Cooper (1920) for *G. catostomi*.

The descending canals pass back into the posterior tip where they empty into a large excretory vesicle. This vesicle receives a number of tubes, the surface in cross section appearing serrated. The cavity is

about 166 by 75  $\mu$  in width and passes ventrally, growing smaller until a size of 60 by 25  $\mu$  is reached. The vesicle then tapers for 120  $\mu$  and passes to the outer ventral surface, through a canal 108 to 110  $\mu$  long by 36  $\mu$  wide. This canal is lined with cuticula and the entire vesicle is embedded in the subcuticular mass, which is characterized by a mass of parenchymal cells and the network of strands in which they lie.

There is one structure which appears in the neck and base of the scolex which will be described at this point, although the exact relation to the excretory system is doubtful. As the neck is reached and the excretory canals begin to branch profusely there appears an increase of the cells of the medullary parenchyma. These in turn give way anteriorly to a great number of large sac-like, irregularly-shaped bodies the granules of which take an eosin stain. Numerous branchings of the inner longitudinal muscular system can be traced through to these sac-like bodies. This condition continues on up into the mid portion of the scolex, where these bodies disappear. The function of these gland-like bodies is unknown. Two small ducts are evident which assume the position taken by the vitelline ducts in the posterior portion of the body. These ducts are situated laterally midway between the dorsal and ventral surfaces 15 to 25  $\mu$  from the lateral inner muscles of the longitudinal system. If they are connected with the excretory system they may function in the expansion of the scolex. Another possibility remains, these may be glands of the scolex, secreting fluids which aid the parasite in boring through the mucosa of the intestine of the host.

The nervous system is first seen in the scolex where the ganglia fuse. Two main branches can be traced posteriorly for a short distance, but they are soon lost.

The unusually large testes, averaging 0.228 mm. by 0.157 mm., number between 300 and 325 in an adult. The average number is between 312 and 318. This fact was determined by actual count of several specimens and by the estimation of the number of several more. A maximum of 0.298 mm. and a minimum of 0.192 mm. constitute the range of the main axis of the testes. The width shows a similar variation, for a maximum of 0.204 mm. and a minimum of 0.120 mm. were recorded. These figures are based upon the measurements of numerous testes, fifty of which are taken as typical examples. The longitudinal axis extends dorso-ventrally in most cases. It is possible, however, to occasionally find a form in which the main axis extends laterally. The easily recognized testes do not begin until approximately the middle of the body is reached. They are confined to the medullary parenchyma by the inner longitudinal muscles and the vitellaria. The latter are typically found scattered about the testes in a circle. The vitellaria are of such a large size, however, that they are readily confused with testicular tissue. Frequently



four of five testes, rarely six, are found in the same section and are usually grouped in pairs (Fig. 83). There are three rows of testes each of which may be broken into a dorsal and ventral portion, making three dorsal and three ventral. When the testes first begin they are not present in such great numbers, usually only two or three appearing together, and these will be both dorsal and ventral. Occasionally a degenerating testis will be found. Two such were noted in one sexually mature specimen. Evidently the spermatozoa had been passed off and the remainder of the tissue underwent degeneration until little but the vacuity which had housed the testis remained. The testes extend posteriorly, interspersed with vitellaria until nearly opposite the cirrus sac. Those in the middle rows end first in order to make room for the convolutions of the vas deferens.

The vas deferens begins in the region of the first testis as a minute duct running an irregular course through the center of the body. As it proceeds posteriorly it gradually increases in size. Like the other Cestodaria the vasa efferentia are indistinguishable. As the testes increase in numbers the zig-zag course of the vas deferens is augmented by smaller tubes which connect with the outer rows of testes. These are perhaps more logically called *vasa deferentia secundaria*, for they are distinctly a part of the vas deferens system. As the vas deferens approaches the mid-testicular region the walls measure 5 to 7  $\mu$  and the diameter of the tube itself is 6 to 8  $\mu$ . This makes the vas deferens easy to trace as it has a total width of 16 to 25  $\mu$ . As it approaches the vicinity of the cirrus sac the testes and vitellaria gradually disappear from the center of the parenchyma, leaving the medullary parenchyma free from these structures in the shape of an inverted "V". This region is filled with the swollen convolutions of the vas deferens. It is filled with the spermatozoa and the wall is much thinner. The vas deferens, after making numerous convolutions, passes dorsally and medianly and enters a narrow muscular tube, the ductus ejaculatorius, which extends for 0.7 mm. before emptying into the seminal vesicle.

The seminal vesicle runs diagonally towards the ventral surface, the more dorsal portion being anterior. The vesicle, 0.28 mm. long and 0.19 mm. wide, contains a cavity 0.16 mm. by 0.04 mm. the latter surrounded by circular muscles. These muscles function in the ejaculation of the spermatozoa through the remainder of the ductus ejaculatorius and the cirrus. The former extends for 0.5 mm. from the seminal vesicle to the cirrus sac. It is thick walled with a diameter of 24 to 36  $\mu$  and is surrounded with circular muscles which aid in the ejaculation of the spermatozoa. The ductus ejaculatorius, therefore, has a total length of about 0.12 mm., 0.7 mm. before the seminal vesicle and 0.5 mm. after. This duct runs ventrally and enters the cirrus sac from the dorsal side (Fig.

29). It penetrates the end of the cirrus sac, instead of laterally as is the case in *Monobothrium wagneri*.

The cirrus sac is characteristic for the species and lies in a diagonal plane at an angle of 45 degrees with the vertical. It is embedded in the subcuticular mass which extends up into this region. The musculature is weak and the circular muscles extend about the cirrus; a few fibers run down into the tip of the papilla. In all the specimens examined this papilla was extended, although it might seem as though it were the papilla of an eversible cirrus. Such condition, however, seems doubtful since the musculature measuring barely 12 to 36  $\mu$  in width is so weak (Fig. 39). The breadth of the extruded portion, or papilla, is 0.293 mm. and the length approximately 0.233 mm. The diameter of the canal penetrating the papilla is 0.01 mm., while that of the cirrus sac proper is 0.03 mm. If the extra muscle fibers extending to the tip of the papilla are included the maximum width is 0.35 mm. The maximum length of the cirrus sac proper is 0.39 mm. and the "urethra" 0.36 mm. The thickness of the lining of this tube is 9 to 12  $\mu$  in the upper half and 4 to 7  $\mu$  in the lower portion of the cirrus sac. The lining appears to be a continuation of the cuticula.

The course of the spermatozoa is nearly the same as that described for other species of *Monobothrium*. The spermatozoa leave the testes, enter the *vasa deferentia secundaria* and thence pass to the vas deferens proper. Here they pass posteriorly and are stored in the lower part of the vas deferens. At the time of sexual activity the spermatozoa are drawn through the ductus ejaculatorius into the seminal vesicle by the action of the circular muscles surrounding it, out through the ductus ejaculatorius and into the cirrus sac and thence to the outside. In the case of self-fertilization the spermatozoa would pass into the genital cloaca, and into the vagina where they would be stored temporarily.

The female reproductive system is composed of vitellaria, ovary, ovarian reservoir, oöcapt, oviduct, oötype and shell gland, uterus and vagina. The vitellaria are found in the anterior portion of the body and lie entirely anterior to the cirrus sac. There are no post-ovarian vitellaria. These glands begin at the end of the neck region 4 to 5 mm. from the tip of the scolex. They extend posteriorly as far as the cirrus sac. Their position is quite characteristic of the Caryophyllaeinae in that a ring is formed about the testes. In this species the inner longitudinal muscles lie externally to the vitellarian circle. These glands are large and resemble the testes in size and shape. They range in size from 0.145 mm. to 0.180 mm. in length by 0.096 mm. to 0.144 mm. in width and are present in great numbers; there are between 720 and 740 in the sexually mature adult. This is based upon actual count of sections and is checked by the mathematical calculation of the number present. The vitelline

ducts are lateral and lie midway between the dorsal and ventral surfaces, just within the inner longitudinal muscles (Fig. 83). These ducts continue posteriorly and receive many smaller ones from the vitellaria themselves. The origin of such ducts may be seen in figure 79, where the tubule takes its origin from the middle of the vitelline follicle. Several follicular tubules unite to form the vitelline ducts. In the region of the ovarian commissure the vitelline ducts pass ventrally on the anterior side of the commissure and then turn medianly where they join and pass ventrally to emerge from beneath and join the vaginal-oviducal canal to form the uterus.

The H-shaped ovary measures 0.8 to 1.0 mm. in length; it is follicular and has a prominent ovarian commissure, the median portion of which functions as an ovarian reservoir. The commissure measures 0.49 mm. in length and has a diameter of 0.19 to 0.3 mm. The ovaries begin 0.48 mm. posterior to the female genital atrium and extend posteriorly until the body becomes pointed.

The oviduct is separated from the ovarian reservoir by the oöcapt. In it is a distinct layer of circular sphincter muscles. These measure 0.048 mm. in cross section. These sphincter muscles control the release of the ova. The oviduct extends ventrally until it meets the vagina and later the vitelline duct. The vagina runs anteriorly and dorsal to the oviduct and ventral to the main portion of the uterus. Just before joining the oviduct the vagina is surrounded by circular muscles 2 to 3  $\mu$  thick under which is a thin non-cellular layer 2.1  $\mu$  thick and above lie the muscle cells 15.9  $\mu$  wide. The width of the entire cavity is 10.6  $\mu$ . There is no distinct receptaculum seminis. As the more anterior portion of the vagina is reached the lining measured 0.9  $\mu$  and the circular muscles 5.3  $\mu$ . This empties after a relatively straight course into the cloaca from the side, and thence passes to the exterior.

The combined oviduct and vagina meets the common vitelline duct within the confines of the oötype. Here the tube is very narrow and the oötype is made up of numerous loose, glandular cells. Ducts originating from the oötype empty into the vitelline ducts before they reach the vagina. These ducts arise from single cells, which appear in the oötype as large glandular cells. These cells may secrete something which aids in the formation of the shell of the ovum. It is probable that these cells and their secretions must have some function which is connected with that of the formation of the shells for the ova, since the vitelline material and the fertilized ova all appear at this spot.

The oötype soon permits the convoluted uterus to broaden slightly as it passes posteriorly. After reaching the posterior limits of the oötype the uterus proceeds anteriorly and passes from the oötype becoming thin walled. This duct turns back upon itself and zig-zags back and forth



behind the arms of the ovary, passing from the right to the left sides in three convolutions. The uterus then runs anteriorly, the main limb passing dorsally to the ovary. Anterior to the ovarian commissure it becomes thick-walled and lined with pear shaped cells, characteristic of the uterine glands. The uterus makes several loops and convolutions, passing from one side to the other before it empties into the cloaca. Ninety to 100  $\mu$  before the emptying of the uterus into the vagina, the thick walled cells become less and circular muscle bands 3 to 5  $\mu$  thick take their place. The functions of these muscles are two fold, in the first place they serve to keep the eggs from being discharged until the time is propitious for their release, and secondly they serve to keep the distal end of the uterus closed at the time the spermatozoa are passed into the vagina (Fig. 39).

The female cloaca is formed by the union of the vagina and uterus. The latter enters from the right side into the vagina which runs ventrally from a more dorsal position. The opening of the uterus is 0.12 mm. wide at its point of entrance into the cloaca. The vagina leaves from a dorsal and posterior position. It is surrounded throughout its entirety by circular muscles. The cloaca passes ventrally for 0.19 mm. where it opens into a fairly large atrium situated posteriorly to the papilla of the cirrus. It measures 0.24 mm. by 0.96 mm. at its widest place. The minimum width is 0.025 mm (Fig. 39). The distance from the middle of the papilla to the center of the atrium is 0.19 mm.

The eggs of this species are fairly large, ovoid and average 57.2 by 30.4  $\mu$ . Measurements were made of the eggs in sections many of which were at different developmental stages. The eggs range from 53 to 58  $\mu$  in length by 28 to 33  $\mu$  in width.

According to the revision of the genus *Monobothrium* the form which has just been described clearly falls into this genus. The scolex is nearly structureless, being rounded anteriorly and possessing 6 shallow longitudinal grooves and a terminal introvert. The ovary is "H" shaped and compact while the cirrus and utero-vaginal atrium open together into a shallow eversible cloaca; the male system is separated from the female by an annular pad (male genital papilla?).

There has only been a single species described as belonging to this genus, *Monobothrium wageneri* (= *M. tuba*). The new species, *M. ingens*, Hunter (1927) has a maximum length of 45 to 50 mm. which is greater than the 22 to 24 mm. recorded by Nybelin (1922:118) and the maximum length of 33 mm. noted by Sonsino (1891) for *M. wageneri*. In *M. ingens* the cuticular, outer and inner longitudinal muscles are present clearly dividing the tissue outside the inner longitudinal muscles into cortical and subcuticular layers. The testes have a maximum diameter of 0.19 to 0.29 mm. and number 300 to 325 in comparison with *M. wageneri* which has testes measuring 0.16 to 0.18 mm. The cirrus sac in the latter measures 0.40 to

0.45 mm. long by 0.28 mm. broad which is in marked contrast to a maximum length of 1.48 mm. and a breadth of 1.3 mm. recorded for *M. ingens*. In all of the specimens examined the cirrus sac was found to lie at an angle of nearly 45 degrees with the vertical. The genital atrium is typical of the genus and both possess the characteristic annular pad, or male papilla (?). The vagina in both cases is relatively straight, neither one forming a distinct receptaculum seminis. The oöcapt arises on the mid line and not laterally as in *M. wagneri*. The vitellaria in the latter are small, measuring 0.07 to 0.1 mm. in comparison with 0.14 to 0.18 mm. for the former. The oötype and shell gland has a diameter of 0.5 mm. in *M. wagneri* and of 0.4 to 0.75 mm. in *M. ingens*. The eggs of the former are much larger and measure 75 to 78  $\mu$  in length and 48  $\mu$  in width compared with a length and breadth of 53 to 58  $\mu$  and 28 to 33  $\mu$  respectively in *M. ingens*.

#### GENUS GLARIDACRIS COOPER 1920

Generic diagnosis: Caryophyllaeinae with three pairs of loculi or bothria on well defined scolex, which may or may not form a definite terminal disc. Cirrus opens on ventral surface or into a shallow, non-eversible genital atrium. Ovary "H" shaped and entirely medullary. Coils of uterus never extend anteriorly to cirrus sac, and reach a maximum longitudinal length of one third that of testicular field, usually less. Terminal excretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in digestive tract of the Catostomidae.

Type species: *Glaridacris catostomi* Cooper 1920.

To include:

- (1) *G. catostomi* Cooper 1920.
- (2) *G. hexacotyle* (Linton 1897).
- (3) *G. laruei* (Lamont 1921).
- (4) *G. confusus* Hunter 1929.

In earlier papers of Woodland (1923, 1926) this genus is deleted and the type species was placed provisionally in the genus Caryophyllaeus. Since that date it has been shown that the genus is really valid and that two other species also fall into this group, *G. hexacotyle* and *G. laruei*. The addition of a fairly common new species to this genus, *G. confusus*, increases the total of valid species to four and erases the possibility of this genus being deleted. It is significant and interesting to note that this genus is apparently confined to this continent as there have been no other records reported even though a number of new species have been described.

#### GLARIDACRIS CATOSTOMI COOPER 1920

[Figs. 2, 25, 44, 45]

1920: <i>Glaridacris catostomi</i>	Cooper 1920: 5-24
1923: <i>Caryophyllaeus catostomi</i>	Woodland 1923: 435-472
1924: <i>Glaridacris catostomi</i>	Johnston 1924: 347



1925: <i>Caryophyllaeus catostomi</i>	Moghe	1925: 232-235
1926: <i>Caryophyllaeus catostomi</i>	Woodland	1926: 56
1927: <i>Glaridacris catostomi</i>	Hunter	1927: 19

Specific diagnosis: With the characters of the genus. Adults up to 25 mm. in length with a maximum breadth of 1 mm.; may be buried in pits in mucosa, altho this condition is more typical of the larvae. Scolex short, broad and chisel-shaped, length varying between 0.3 and 0.45 mm. Neck distinct, slightly narrower than body which is flattened dorso-ventrally and bears a conspicuous genital atrium. Cuticula 7 to 11  $\mu$  thick, subcuticula 12 to 16  $\mu$  in depth; this in turn is bounded internally by outer longitudinal muscles. These muscles separate it from the cortical parenchyma which has a depth of 70 to 84  $\mu$ . Both inner and outer longitudinal muscles are present and prominent. The testes number between 405 and 420 and are irregularly ellipsoidal with a maximum diameter of 0.12 to 0.19 mm. Cirrus sac ovoid to spherical, occupies the entire medullary parenchyma, possessing a maximum diameter of 0.4 to 0.6 mm. Common genital atrium conspicuous, 0.4 to 0.5 mm. long, 0.7 to 0.16 mm.; female reproductive system opens 0.13 mm. posterior to that of the male. Vagina median, ventral, convoluted and forms an indistinct receptaculum seminis. Wings of the ovary 0.65 to 0.9 mm. long; prominent ovarian commissure 0.4 mm. in diameter. Vitellaria with maximum diameter of 0.2 mm.; expanded common vitelline duct functions as vitelline reservoir. The excretory system has 8 to 10 pairs of canals with terminal excretory bladder measuring 0.25 by 0.05 mm. Eggs operculate, 54 to 66 by 38 to 48  $\mu$ .

Host: *Catostomus commersonii*, Douglas Lake, Mich.; Burntside Lake, Minn.; Lake Erie, Silver Creek, New York.

Type: Cooper's original slides in the collection of Dr. Henry B. Ward. No. 25. 137.

Host	Locality	Collector	Authority
<i>Catostomus commersonii</i> (Lacépède)	Douglas Lake, Mich.	A. R. Cooper	Cooper 1920: 5-24 Hunter (the present paper)
<i>Catostomus commersonii</i> (Lacépède)	Burntside Lake, Minn.	H. E. Essex	Hunter (the present paper)
<i>Catostomus commersonii</i> (Lacépède)	Lake Erie, Silver Creek, N. Y.	G. W. Hunter, III	Hunter (the present paper)

*Glaridacris catostomi* was originally described by Cooper (1920) and designated as a new genus and species. At that time the author thought that this form was the first to be described from this continent, and was in ignorance of the two forms noted by Linton in 1893 and 1897. Some years after publishing this description all of the slides and material were turned over to Professor Henry B. Ward, who was kind enough to loan the specimens to me for comparisons with other material. Since the original work was found to be at fault in several instances it seemed advisable to publish the corrected description ensemble.

The material was obtained at the Douglas Lake Biological Station of the University of Michigan, where a total of 36 specimens of the host, *Catostomus commersonii* (Lacépède) was examined. The younger fish ranged in size from 90 to 115 mm. and were obtained by seining them out of the Maple River; these were uninfected with Cestodaria. The adults, however, were taken in fyke nets from the lake and 11 of the 26 were parasitized.

Most of the larvae and all of the adults were found free in the stomach or the intestine, but as Cooper (1920: 6) says, many of the larvae were found, attached to the bottoms of deep pits in the mucosa of the pyloric region of the stomach. These pits were not mere depressions of the wall of the stomach but actual cavities, . . . bordered by a pronounced annular thickening of the mucous membrane and as much as 2 mm. in diameter. Larvae ranging in size from almost the smallest met with to those near the adult stage in development were tightly crowded into these pits and at the same time strongly contracted longitudinally.

This description is typical of the larvae of this species.

Inasmuch as the musculature of this species is well developed the contraction of the individuals varied considerably but the length of the adults ranged from 5 up to 25 mm. and from 0.4 to 1 mm. in maximum breadth. In the larvae the scolex shows little or no differentiation and the body tapers behind to a blunt tip at the posterior extremity. Often the body appeared wrinkled due to the contraction. In adults the scolex presents several different shapes, the typical shape appearing in figure 2. The neck lies behind the scolex and, as is typical for the members of this genus, is the narrowest portion of the body. This region varies from 1.5 to 2.5 mm. in length. The body broadens posteriorly and the posterior extremity is slightly indented at the point where the excretory vessels open to the outside.

The scolex of the adults is characterized by the presence of three loculi on the dorsal and ventral surfaces, and these are accentuated by the muscle bands which extend towards the distal end forming a broad tip, which is somewhat chisel-shaped. It differs from *G. hexacotyle* in not having the loculi unite to form a single, pointed conical apex. The length of the scolex varies between 0.30 and 0.45 mm.; the width between 0.45 and 1.10 mm.; and the depth (posteriorly) between 0.50 and 0.75 mm. In the base of the

scolex are found the eight large fasciculi of the inner longitudinal muscles. Posterior to this lies a large mass of cells characterized by large nuclei; the cytoplasm contains numerous granules having an unusual affinity for counterstain. These are probably glandular for they send out long processes in a diagonal direction to the cuticula.

The cuticula varies in thickness from 7 to 11  $\mu$  and is bounded medianly by the relatively heavy basement membrane extending one-sixth the thickness of the entire layer. The remainder of the cuticula has something of the appearance of a reticulum described by Cooper (1920:8-9) as follows:

This reticulum is in reality a meshwork of fine canaliculi which freely pierce both limiting membranes, thus giving them the appearance in tangential sections of fine sieves. Nowhere is the cuticula modified to form spinelets nor distinct cirri, although over the scolex it is considerably folded and irregular, the outer membrane being all but absent, especially within the suckers.

The subcuticula is composed of large flask shaped cells, having rather large nuclei. The entire layer is 90 to 100  $\mu$  in thickness. The spherical to ovoid nuclei are crowded together, measure 16 to 18  $\mu$  in greatest diameter. The nucleoli are spherical. This area is considered as one by Cooper, but is divided into two parts. The outer or subcuticula extends 15 to 30  $\mu$  from the cuticula and is separated from the more median cortical parenchyma by the band of outer longitudinal muscles. This division is rather arbitrary and does not occur in all of the species studied, but when it does occur it should be noted and used. The main longitudinal canals of the excretory system are confined to the cortical parenchyma. The cells of the parenchyma are distinctly different from those of the subcuticula, the distinction being largely one of contrast with the subcuticula cells. The former take the stain deeply while the latter are marked by their clear, non-granular cytoplasm.

The musculature is composed of two sets, the cuticular and the parenchymatous. This parasite has both sets well developed. The circular muscles of the cuticula are slightly over 1  $\mu$  in thickness and lie close beneath the basement membrane. Inside this layer are found those fibers belonging to the longitudinal cuticular system. There are 2 or 3 and sometimes more, in a fasciculus, and Cooper (1920) reports that sometimes these muscles intermingle with those of the outer longitudinal system. The parenchymatous muscles are very prominent. The outer longitudinal muscles are arranged in small bundles, each containing upwards of fifteen fibers in a bundle. The size of these bundles is more uniform than the inner longitudinal groups and they lie 15 to 30  $\mu$  from the outside. Posteriorly these fibers and those of the longitudinal cuticular system intermingle as they become embedded in the wall of the excretory bladder. The muscles of the inner longitudinal system are by far the most prominent; they are found 60 to 100  $\mu$  from the outside and there are up to 25 fibers in the fasciculi.



In the neck these are collected together so that eight large bundles are formed (cf. Fig. 61). Cooper (1920:11) describes these as follows:

. . . the eight large bundles of inner longitudinal muscles, mentioned above, are arranged so that four form two sagittal pairs situated towards the lateral faces, while the other four, somewhat larger ones form two other sagittal pairs, each about half way between the nerve trunk and the median line. These are distributed in a radiating manner to the corresponding portions of the tip of the scolex, the median pairs going to the ridges between the loculi and the neighboring pairs of the latter. On the whole their attachment is similar to that of the main longitudinal group in *C. tuba* and *C. laticeps*, as described respectively by Monticelli (1892) and Will. The outer longitudinal muscles are more numerous on the lateral surfaces of the scolex than opposite the suckers, to the cuticula of which they are easily traced. The loculi are also provided with a few scattered radiating fibers, lying in both the longitudinal and transverse directions, and comparable to those used in the Pseudophyllidea for the enlargement of the bothria. They are, however, of much less functional importance in that connection than the sagittal and transverse fibers, which are somewhat larger and more numerous than in the middle of the worm. In fine, the musculature of the scolex is poorly developed as compared with that of *Bothriocephalus*, s. str., for example, which fact is shown in the great diversity of shapes of the organ in preserved material.

The nervous system was worked out by Cooper in his original description and as no errors were found the description is quoted verbatim.

The nervous system consists of a pair of ill-defined longitudinal trunks and two equally indistinct and diffuse terminal ganglia situated in the scolex, into which they pass. The main strands can be followed more or less easily in material not especially treated to demonstrate them only in the neck region. There, . . . they are situated symmetrically in the median frontal plane within the trapezium formed by the two pairs of main longitudinal muscle bundles, much closer, however, to the lateral pair than to the more median pair. They supply these muscles with large branches. Whereas in the neck they are fairly uniform in diameter—which varies from 18 to 30  $\mu$ —behind the most anterior vitelline follicles they become quite irregular in transection, all but disappearing in places. In the middle of the worm and posteriorly they seem to break up into a diffuse plexus lying just within the subcuticular cells, that is, among the numerous bundles of the inner longitudinal muscles. No collateral strands such as the eight described by Will for *C. laticeps* were seen in this form.

In the base of the scolex these chief nerve strands expand considerably in the dorso-ventral direction and become united by a few transverse fibrils. Farther towards the tip, however, each of these enlargements divides into two parts sagittally, and each of the latter unites with its fellow of the opposite side by a loose strand of transverse fibrils, so that two anteriorly directed loops are thus formed. On the whole the nervous system is comparatively poorly developed, since not only the chief strands but also their connections in the scolex are composed of very fine, indistinct and loosely arranged fibrils.

The excretory system consists of ascending and descending canals in pairs; and therefore do not differ from the typical systems. Anteriorly there are eight main channels, located three on each surface and one at each lateral margin. As the neck is reached the tubes break up into numerous plexuses. These canals and canaliculi invade all parts of the subcuticula and the cortical parenchyma. About 1 to 1.3 mm. from the tip of the scolex two branches leave the plexus above and below the nerve cord and unite "on the medial side of the latter to form one vessel. In these positions

the two vessels thus formed pursue spiral courses forward and apparently unite close behind the nerve commissures mentioned above." (Cooper.) The main descending canals of this system find their way to the unusually large excretory vesicle. It measures 0.25 mm. in length by 0.05 mm. in width, and appears as an invagination of the hinder portion of the parasite, for the wall is composed of a lining of cuticula identical with that found on other surfaces. A few circular muscles were detected about this vesicle; the main muscles of both longitudinal systems also give off fibers which are embedded in the walls of the vesicle which empties on the median ventral surface at the posterior tip of the body. True flame cells were not present. In their place are the renal corpuscles which were first described by Cooper (1920:13-14). Each cell is composed of a distinct nucleus and nucleolus, with a cytoplasm which is highly vacuolated. The bulk of the cytoplasm lies about the nucleus with only strands radiating out to the wall of the cell, which are continuous with the wall of the canaliculus leading to the ascending canal. The probable mechanism by which these cells function is discussed on page 13 (Cooper 1920).

The male reproductive system is of interest in several respects. The testes are very numerous and rather large. They are completely surrounded by the vitellaria and are irregularly ellipsoidal in shape numbering 405 to 420 in the normal adult. This number was checked by actual count and also by an estimation of the number present. The method is described in detail on page 11. In the more anterior portion of the body the testes are smaller than they are posteriorly; they are arranged in two rows one of which is dorsal and the other ventral. There are two or three testes in each row (Fig. 45). Various stages of spermatogenesis were visible in the different testes and also it was possible to find some of the spermatozoa in the more distal portions of the vas deferens. This is contrary to Cooper's findings but they are clearly present in one of the adults which were sectioned by the author. At the same time eggs were present in the uterus. In normal conditions the spermatozoa mature first.

The vas deferens is formed by the union of various branches of the vas deferentia secundaria which extend from the testes to the vas deferens. Each tube will tap three or sometimes four testes and bring these products to the vas deferens. As the cirrus sac is approached the vas deferens forms a loose, triangular mass of coils which measures about 0.32 mm. in length, 0.36 mm. in depth, and 0.28 mm. in width. A short distance before passing into the cirrus sac the vas deferens becomes narrower and enters the muscular ductus ejaculatorius. This almost immediately expands to form the seminal vesicle which structure is about 0.30 mm. in length and has a diameter varying between 0.065 and 0.090 mm. The wall of the duct consists of an epithelium syncytial in nature, in which are embedded widely separated nuclei. About this layer lies the muscles which are composed principally of



circular muscles and a few oblique fibers scattered among them (Fig. 25).

The vas deferens enters the cirrus sac from the anterior dorsal surface. At the point of entrance it measures about  $30\ \mu$ , this soon expands in the dorsal third of the cirrus sac to form a secondary, but probably temporary, seminal vesicle with a maximum diameter of  $60\ \mu$ . The size soon diminishes and the cirrus proper is reached. The cirrus occupies the lower half of the cirrus sac and has a diameter of 60 to  $65\ \mu$ . The lining of cirrus is smooth cuticula which is continuous with that of the ventral surface of the worm, and above this may be found the circular muscles in slightly greater number than about the walls of the ductus ejaculatorius. The cirrus sac occupies the whole of the medulla of this region dorso-ventrally and almost all of it laterally. It is ellipsoidal in shape and its maximum diameter varies between 0.4 and 0.6 mm. The wall is composed of muscular fibers surrounding the sac and extending in all directions. A few of the dorso-ventral fibers pass from the top of the sac into the dorsal body wall and some from the lateral position of the sac pass to the ventral body wall. Within this layer are found numerous retractile muscle fibers which are attached to various parts of the cirrus; their exact insertion could not be ascertained with accuracy from the material available. The myoblastic nuclei of the retractile muscles as well as a small amount of parenchymal tissue is also present.

The female genital atrium lies 0.5 to 0.13 mm. posterior to that of the male and opens into the common atrium (Fig. 25). This common atrium is about 0.45 to 0.55 mm. in largest diameter and has a depth of 0.7 to 0.16 mm. Because of its relatively great length it does not appear to be particularly deep. The female genital atrium lies posterior to the male, and is much more conspicuous, having a diameter of 0.12 to .168 mm. at the point of entrance into the common atrium and a maximum depth of 0.2 to 0.3 mm. The opening is crescentic and narrows as it progresses medianly to 0.4 to 0.7 mm. part of the way up. The cortical parenchyma surrounds the female genital atrium to a marked degree so that the outer longitudinal muscles are forced medianly at this point. The uterus enters the female atrium, 0.2 to 0.3 mm. from the surface in the median portion of the body laterally and from the left. The vagina empties slightly nearer the surface than the uterus and on the opposite side (Fig. 44).

The ovary is irregularly lobate and is situated about half way between the genital atrium and the posterior body tip. (See Fig. 25.) It is from 0.65 to 0.9 mm. in length and with the prominent ovarian commissure forms the "H" so characteristic of this group. In cross section the ovary occupies nearly the entire medullary field, except for the uterus, which lies dorsal and median to it. The vagina lies beneath and the vitelline ducts parallel each ovarian wing which has a depth of 0.4 to 0.45 mm. and a wing width of 0.2 to 0.25 mm. The ovarian commissure leaves about the center of the

wing of the ovary and extends medianly. It is spherical in cross section and has a maximum diameter of 0.4 mm. The median portion of this commissure functions as an ovarian reservoir and contains ova ranging in size from 13 to 18  $\mu$  in length by 10 to 15  $\mu$  in width. The majority of them are nearly spherical and measure in the neighborhood of 15  $\mu$ .

The vitellaria are found in two separate and distinct fields, one extending from the neck to the cirrus sac and the second confined to that portion of the body between the posterior coils of the uterus and the posterior extremity of the body. In the anterior portion of the body they form a distinct layer about the testes and vary in number from 8 to 15 in cross sections (Fig. 45). These glands become slightly larger posteriorly and have a maximum diameter of 0.2 mm. The process of the formation of the yolk cells is clearly described by Cooper (1920:18-19) as follows:

The cytoplasm of the small peripheral primordial cells from which they develop is very compact, and consequently stains deeply as does the nucleus. Numerous vacuoles appear in it and quickly enlarge, so that in the intermediate stages the nucleus appears to be suspended in the center of the cells by protoplasmic strands radiating from it to the cell membrane . . . . These strands become modified into numerous, spherical deutoplasmic granules, migrate outward and eventually come to lie just inside the cell-membrane. In the proximal part of the uterus, where from four to six vitelline cells are seen to be associated with each fertilized ovum in the formation of the egg, the nucleus enlarges still more and becomes more transparent, while the cell-wall gradually breaks down, thus liberating the vitelline granules. The enlarged nuclei remain intact, however, during the passage of the egg through almost the whole length of the uterus.

The vitelline ducts are four in number, but are reduced to two as the cirrus sac is approached. These two ducts take a median position on each side of the vagina and pass posteriorly. They measure 7 to 50  $\mu$  in diameter depending upon the presence or absence of the vitelline follicles. As the ovarian commissure is approached the two vitelline ducts join to form a common vitelline reservoir lying dorsal to the commissure. The vagina lies above, and dorsal to it the uterus. The reservoir ranges in size between 30 and 100  $\mu$ . Upon reaching the ovarian commissure the common vitelline duct is joined by two small ones from the post-ovarian vitellaria. Immediately the common vitelline ducts divide into an upper and lower reservoir, one end of which is blind. The single vitelline duct passes over the dorsal surface of the posterior edge of the ovarian commissure and becomes very narrow, the diameter dropping from 20  $\mu$  to almost nothing. At this point the oötype is penetrated and as the duct passes towards the center of this structure several minute ducts were found to empty into it from various parts of the oötype. Soon this canal continues dorsally and to the left and empties into the combined vaginal-oviducal canal, or fertilization chamber. The course of the vitellarian duct within the oötype is outlined by the myoblastic nuclei which are found 6 to 8  $\mu$  from the canal itself, and surround the few thin muscles about the canal.

The vagina passes posteriorly from the female genital atrium just beneath the coils of the uterus. The diameter near the point of origin is between 50 and 55  $\mu$ ; this is reduced to 30  $\mu$  or less as the canal passes posteriorly. The vagina is lined with a layer of cuticula about 5  $\mu$  in thickness which in turn is surrounded by numerous circular muscles whose myoblastic nuclei form a distinct layer about 10  $\mu$  from the fibers. The canal is convoluted and as it passes posteriorly is pushed dorsally to the center as the ventral portion of the ovary becomes filled with the ova to form the ovarian reservoir. As the vitelline ducts expand the duct is pushed further dorsally; soon the vagina, measuring about 25 to 35  $\mu$  in diameter, passes to the right and the vitelline duct comes up and fills the left median portion of the medullary parenchyma. An indistinct receptaculum seminis is formed and this soon gives way to the narrow vagina, now 7 to 12  $\mu$  in diameter, which dips ventrally over the posterior edge of the ovarian commissure to become enveloped in the oötype (Fig. 44).

The oöcapt arises from the median posterior surface of the ovarian commissure. It measures 29 to 32  $\mu$  in cross section and the canal is surrounded by circular muscles 10  $\mu$  in thickness forming the sphincter which controls the release of the ova from the ovarian reservoir. The oviduct is extremely long, about 0.2 mm. in length and has a diameter of 21 to 23  $\mu$  which is reduced to 9 or 10  $\mu$  before joining the vagina which passes up from a more ventral position to form the fertilization chamber. This oviducal-vaginal canal passes to the right, is joined by the single vitelline duct, dips ventrally, just keeping within the bounds of the oötype and curves back on itself to leave the oötype near its posterior extremity. The oötype is rather prominent and has a maximum diameter varying between 0.38 and 0.42 mm.

The uterus leaves the oötype posteriorly and passes through several convolutions, the walls being lined with syncytial epithelium. It soon enlarges and becomes filled with eggs. The size increases and its wall becomes thinner until it turns anteriorly to pass dorsally over the ovarian commissure. As the posterior tip of the ovary is passed the uterus becomes surrounded by a mass of unicellular and club shaped glands. The uterus is surrounded with only a few scattered muscles until the region of the female atrium is reached when the glands give way to the myoblastic nuclei which surround the muscles of this region. Inasmuch as Cooper examined fresh eggs from this species his description is repeated verbatim.

The mature fresh eggs, when examined in normal saline solution, were found to be ovoid in shape and from 54 to 66  $\mu$  in length by 38 to 48  $\mu$  in width. The shell is from 2 to 3  $\mu$  in thickness, and is provided at its larger end with a small button-like boss and at its smaller end with an operculum from 12 to 16  $\mu$  in diameter.

*G. catostomi* because of the position of its sexual apertures and ovary,



the annular arrangement of the vitellaria about the testes which are surrounded by the inner longitudinal muscles, falls into the Caryophyllaeinae. The genus Caryophyllaeus is characterized by a broadened or curled anterior extremity which is not specialized into a scolex, and the absence of an external seminal vesicle. In this last respect it differs from *G. catostomi*. Other differences of the scolex and genital atrium keeps this species from the genus Monobothrium, while it differs from Caryophyllaeides in the lack of specialization of the scolex, type of genital atrium and the presence of the uterine coils anterior to the cirrus sac. In these three characters it also differs from the genus Biacetabulum, and it is separated from the genus Hypocaryophyllaeus by the presence of the uterine coils anterior to the cirrus sac. Clearly then this species does not fall into Caryophyllaeus, Monobothrium, Caryophyllaeides, Biacetabulum or Hypocaryophyllaeus. However, it does fall into the one remaining group, Glaridacris, for it possesses three pairs of loculi on a well defined scolex, the cirrus opens into a shallow genital atrium while the ovary is "H" shaped and medullary, the coils of the uterus are not anterior to the cirrus sac, there is an external seminal vesicle, and this form is parasitic in the intestines and stomach of the Catostomidae. It differs from the other forms thus far described from this continent in several respects. In the first place *G. catostomi* is clearly separated from the other two species described by the type of scolex, for *G. laruei* possesses the "II" type, and *G. hexacotyle* has six weak loculi, forming a conical apex which distinguishes it from *G. catostomi*. The cuticula of this latter species is 7 to 11  $\mu$  in thickness and is thicker than the 2 to 3 and 3 to 5  $\mu$  cuticula measurements of *G. laruei* and *G. hexacotyle*. Again the number of testes facilitates the determination of the species. *G. catostomi* has 405 to 420 while *G. hexacotyle* and *G. laruei* have respectively 175 to 200 and 60 to 85. The cirrus sac of *G. catostomi* occupies the entire medullary parenchyma, laterally as well as dorso-ventrally thus serving as an excellent means of differentiation. The circular muscles about the cirrus sac are also nearly twice as thick as those found in the other species under consideration. Furthermore, this species possesses a very prominent genital atrium which is 0.4 to 0.5 mm. in greatest diameter and 0.07 to 0.15 mm. in depth. Such an atrium is not characteristic of the other two species belonging to this genus. The female atrium, opening into the common cavity is 0.13 mm. posterior to that of the male in Cooper's form while it is 12 to 19  $\mu$  and 20 to 26  $\mu$  behind that of the male in *G. laruei* and *G. hexacotyle*. The vitellaria surround the testes with 8 to 15 in view in trans-section and the expanded common vitelline duct serves as a reservoir. In this respect it differs from *G. hexacotyle* in which the expanded ducts function as vitelline reservoirs and the anterior group of vitellaria are confined to two lateral fields within the inner longitudinal muscles. *G. catostomi* differs from *G. laruei* and *G. hexacotyle* in the absence of a distinct receptaculum seminis.

The eggs of *G. catostomi* are much larger, ranging between 54 to 55  $\mu$  by 38 to 48  $\mu$ , while those of *G. hexacotyle* and *G. laruei* have a maximum length and breadth of 42  $\times$  30  $\mu$ . The excretory bladder of this species is larger than that of *G. hexacotyle* and *G. laruei*, measuring 0.25 by 0.05 mm. compared with 0.045 to 0.048 by 0.024 mm. for the latter two forms.

Cooper (1920) in his original paper describes two different types of scolices for his new species *Glaridacris catostomi*. To quote:

In immature individuals the scolex, when not strongly contracted, has somewhat the form of a truncated rectangular pyramid with the longer diameter in the transverse direction . . . the edges of the base and the apex protrude markedly, in the latter case forming a terminal disc comparable to that of many of the bothriocephalid cestodes. The dorsal and ventral surfaces of the organs are each divided by two ridges converging towards the apex into three sucking grooves or loculi, of which the middle is best developed and most efficacious during life. It is also the last to become smoothed out with the strong contraction of the whole scolex. The lateral loculi are, furthermore, not in the same plane with the medial one but inclined towards the corresponding ones of the opposite surface so that the edges of the scolex, especially just behind the terminal disc, are often not much thicker than the ridges between the loculi . . . . In adults, on the other hand, the edges of the terminal disc are usually found in preserved material to be contracted to the point of obliteration, so that the whole organ is shaped more like a wedge or chisel with oftentimes rather thick margins. As a matter of fact the scolex of this form assumes a greater variety of shapes than that of any other tapeworm I have yet examined, in which respect it is comparable to the leaf-like anterior end of *Caryophyllaeus*.

Cooper's original vials and slides were placed at my disposal through the kindness of Professor Henry B. Ward. Also some vials of *Cestodaria* taken from *C. commersonii* from Douglas Lake, Michigan were loaned by Dr. George R. LaRue. Upon examination of this material (75 or 80 individuals collected over a period of years) it is apparent that at least two species of *Cestodaria* are present. Under binoculars it is a relatively simple matter to distinguish the larvae of *G. catostomi*. They are thicker, with a greater breadth anteriorly and taper posteriorly to a blunt point. The scolex is structureless and shows little or no differentiation at this stage. At the margin of the last quarter of the body, however, lies the genital atrium, conspicuous even in specimens only 1.9 to 3.3 mm. long. At the same time members of the species *G. laruei* can also be detected with ease. These forms are longer and narrower and possess the type of scolex characterized as the "Π" type because of its resemblance to this Greek letter. These larvae may be further distinguished by the absence of the conspicuous genital atrium which was characteristic of the 25 larvae of *G. catostomi* which were examined. Sectioned material shows other differences between these two species. First the cuticula is vastly different, and this character alone would serve to differentiate them, for on *G. laruei* it never exceeds 2 to 3.5  $\mu$  in thickness and is perfectly smooth. Upon the other hand the cuticula of *G. catostomi* is pigmented, takes a deep blue stain and measures about 25  $\mu$  in depth, except for the scolex where it is reduced to about



4 or 5  $\mu$  in thickness. This layer besides being unusually thick and pigmented possesses rather characteristic depressions extending to within 4 to 6  $\mu$  of the basement membrane. This gives a distinctly serrated appearance in the sectioned material. Another means of distinguishing these larvae from *G. laruei* lies in the fact that the common genital atrium or cloaca is prominent in specimens of less than 2 mm. and even at this stage has a depth of 0.8 to 0.14 mm. The female reproductive organs open in the posterior end of this cavity and the male in the anterior. These figures coincide with the depth of 0.7 to 0.15 mm. noted for the adults. It is evident therefore that Cooper in his original description confused these two forms and that the scolex which he describes for the larval stage is in reality that of *G. laruei*.

*GLARIDACRIS HEXACOTYLE* (LINTON 1897)

[Figs. 3, 19-21, 41, 42, 84]

1897: <i>Monobothrium hexacotyle</i>	Linton 1897: 423-456
1923: <i>Caryophyllaeus hexacotyle</i>	Woodland 1923: 451, 457
1922: " <i>Monobothrium</i> " <i>hexacotyle</i>	Nybelin 1922: 123-124
1925: <i>Monobothrium hexacotyle</i>	Moghe 1925: 23
1926: <i>Caryophyllaeus hexacotyle</i>	Woodland 1926: 56
1927: <i>Glavidacris hexacotyle</i>	Hunter 1927: 20

Specific diagnosis: With characters of genus. Adults 8 to 18 mm. long by 1.03 to 1.2 mm. wide. Ridges between six loculi form a conical apex. There is a small neck as vitellaria and testes extend to base of scolex. Body flattened dorso-ventrally, tapering posteriad; in cross section posterior end appears serrated. Cuticula 3 to 5  $\mu$  thick; subcuticula and cortical parenchyma nearly indistinguishable but 5 to 8  $\mu$  and 12 to 42  $\mu$  thick, respectively. Inner and outer longitudinal muscles present; the latter appear as scattered strands in neck. Oblong, irregular testes numbering 175 to 200; maximum diameter 0.14 to 0.26 mm. Cirrus sac occupies about one half of medullary parenchyma, maximum diameter 0.168 to 0.228 mm.; muscles of organ are 14 to 26  $\mu$  thick. Male and female reproductive systems open into a shallow, common genital atrium; female is 10 to 26  $\mu$  posterior to that of male. Vagina is convoluted, ventral, and forms distinct receptaculum seminis, 60 by 24  $\mu$ . Wings of ovary have a maximum length of 0.8 to 0.9 mm. and width of 0.096 to 0.122 mm. Ovarian commissure "V" shaped, maximum diameter 0.21 mm. Vitellaria with maximum diameter of 0.21 mm. confined to two lateral fields; do not surround the testes. A single duct drains a group of post-ovarian vitellaria. Excretory canals vary between 8 and 10 pairs ending in terminal vesicle 48 by 24  $\mu$ . Parenchyma filled with large number of irregular, glandular appearing cells which pack the medullary parenchyma from the base of the scolex posteriad, gradually thinning out as cirrus sac is reached. Specialized muscle of transverse and dorso-ventral sets form circular muscles just internal to inner longitudinal muscle mass. Eggs, ovoid, 37 to 41 by 23 to 30  $\mu$ .

Host: *Catostomus* sp., Gila and Salt Rivers, Arizona. In intestine.

Paratype: Specimens in Vial No. 4793 of the United States National Museum, Washington, D. C.

Host	Locality	Collector	Authority
<i>Catostomus</i> sp.	Gila and Salt Rivers, Ariz.	—	Linton 1897: 423-456 Hunter (the present paper)

This species was originally described in a very superficial manner, by Linton (1897) as *Monobothrium hexacotyle*. The material was secured by him from the United States National Museum at Washington, D. C. Through the kindness of the United States National Museum a vial of the original material was sent to Professor H. B. Ward. The label in the vial reads as follows "U. S. N. M. #4793. *Monobothrium hexacotyle* Linton. From sucker of Gila River and Salt River, Ariz." Since the original description does not contain a detailed account of the internal anatomy a full discussion will be given in the following pages.

*Glaridacris hexacotyle* is a parasite of moderate length and presents a rather monotonous appearance in external view. There is but a slight widening of the scolex and practically no neck. The length of mature individuals ranges between 8 to 18 mm., while the maximum width of the specimens varies between 1.03 and 1.23 mm. The scolex appears conical even in the contracted state. The base of the scolex is nearly circular, but is divided laterally to form two lobes, one of which projects laterally from the dorsal surface and the other from the ventral. In other words the circle is broken laterally by two indentations which divide the body into dorsal and ventral halves. Each of these lobes is divided by two longitudinal ribs into three loculi, all of which meet at the apex of the scolex to form the conical papilla which may be elongated and then retracted (Fig. 3). The scolex is widest at the base; measurements of the scolices available give a width of 0.507 to 0.608 mm., while the length, taken posteriorly, varies between 0.507 and 0.608 mm. However it should be noted that there is probably more variation in living material for all the scolices were fairly well contracted. When viewed laterally the scolex was narrower and measured between 0.405 and 0.758 mm. In side view it forms a single cone, for the loculi are not readily visible from this position. The neck is very short and shows little differentiation in this species. The width at the narrowest place is between 0.455 and 0.758 mm. while the length posteriorly is 0.2 to 0.3 mm. The body possesses a maximum width of 1.03 to 1.23 mm. and is flattened dorso-later-

ally to a depth of 2 mm. It becomes narrower as the more posterior portions of the parasites are reached. The body width just anterior to the cirrus sac ranges between 0.70 and 0.86 mm. while posteriorly this decreases to 0.60 and 0.76 mm. In the posterior region there are protrusions which are caused by the distended egg-filled uterus. The posterior body tip is bluntly rounded. In several specimens it was possible to secure measurements of extended cirri. These measurements did not exactly coincide with those secured by Linton (1897:427). The extended cirri measured about 0.45 mm. in length, while the width varied from 0.02 to 0.03 mm. at the apex to 0.06 to 0.07 mm. at the base.

The internal organization of this parasite marks it as one of the most unique which have come under my observation. The scolex resembles *G. catostomi* in general shape, but a more careful examination shows it to be markedly different. The base of the scolex appears in cross section to be merely a widening of the neck region. The inner longitudinal muscles which encircle the glandular-like medullary parenchyma become pushed outwards by the swelling parenchymal mass. At this point the inner longitudinal muscles become collected first into two large "V" shaped bundles with the base of the "V" near the lateral wall. These are separated into 8 regions which roughly correspond to the 4 ridges dividing the loculi (Fig. 20). There is also a group on each side of the lateral groove at the base of the scolex. In sagittal and frontal sections it is possible to trace the distribution of these fibers with considerable ease. The bulk of them form the four central groups of muscles, but after running through the ridges between the loculi become largely dissipated and disappear in the basement membrane of the more proximal loculi. A few of the fibers and the bulk of those in the lateral fields pass to the apex of the scolex (Fig. 21).

The presence of dorso-ventral fibers running between the surfaces of the loculi tends to keep this region from expanding (Figs. 19, 21). Similar muscles running at right angles extend through the scolex laterally. (See Figs. 19-21.) Furthermore, there are a few muscle fibers extending in an anterior-posterior direction through the base of the scolex; these keep the base from elongating anteriorly.

The glandular-like medullary parenchyma gives way to the more typical cortical type filled with nuclei and the canals of the excretory system. Here again, as described for *M. ingens* and *C. terebrans*, there are extensions of the ascending canals of the excretory system into the scolex where they break down in the more distal extremities to small canaliculi which freely anastomose. The action of the fluid in these canals is no doubt responsible in a large degree for the extension of the scolex. The presence of numerous cross muscle fibers insures the elongation of the scolex when the fluids pass into the excretory canals by preventing a slight lateral distension.

The integument of this species has not been well preserved and in many



instances the outer layer of the cuticula is absent. The cuticula of this species normally possesses a thin outer membrane, less than  $1\ \mu$  in thickness. Beneath this lies the thicker cuticula proper which is bounded internally by the basement membrane. The circular muscles of the cuticula may be seen in most sections as a very thin band lying just median to the basement membrane. The longitudinal cuticular muscles are more readily distinguished; they lie 2 or 3 in a fasciculus close beneath the circular layer.

The parenchymal muscles of this form are unique and will be considered in the later paragraphs dealing with the musculature. Suffice to say here that the inner longitudinal muscles are not as highly developed as in most forms while the appearance of a few circular muscle fibers complicates the structure. With the presence of these muscles and an increase in the dorso-ventral and lateral musculature there is a coincident decrease in the development of the muscles of the longitudinal system.

This species is further peculiar in that there is no apparent subcuticular layer. The canals of the excretory system which are usually found only in the cortical parenchyma are present close to the cuticula. Furthermore, the median edge of the subcuticula is normally bounded by the outer longitudinal muscles and this band is present only as a few scattered single fibers. The nuclei have the appearance typical of the subcuticula. The scattered outer longitudinal fibers are 4 to  $7\ \mu$  from the longitudinal cuticular muscles and 8 to  $10\ \mu$  from the basement membrane. This entire mass resembles one layer more than two and therefore will be considered as a single layer composed of the subcuticula and the cortical parenchyma. The inner longitudinal muscles are more median in the region of the scolex making the combined subcuticula and cortical parenchyma wider than it is in the posterior portions. It contains the main canals of the excretory system as well as the great mass of dorso-ventral, lateral and a few diagonal muscle fibers.

The medullary parenchyma possesses fewer parenchymal cells and contains a great mass of glandular-like cells. These are more profuse in the neck; they are large and regular in shape, measuring 24 to  $60\ \mu$  by 24 to  $36\ \mu$  in width, and extend from the neck posteriorly as far as the center of the body. Here their numbers begin to decrease. The testes and vitellaria invade this tissue and reduce the reticulum to a mass lying between and surrounding the organs of reproduction (Fig. 21). The testes and vitellaria are confined to the medullary parenchyma by the inner longitudinal muscles.

The musculature of this species is remarkable because of the unusual development of the smaller muscles of the parasite, coupled with the apparent degeneration of some of the prominent muscles. The cuticular system is poorly developed and has been described in the paragraphs dealing with the integument. The muscles of the parenchymal system are usually highly developed and readily discernible both in toto and sectioned

material. In the case of this parasite, however, the outer longitudinal muscles are only faintly visible and appear as single muscle fibers 8 to 10  $\mu$  from the basement membrane. The inner longitudinal muscles also lie relatively close to the cuticula. This system of muscles is between 21 and 45  $\mu$  from the cuticula; these muscles are more median in the anterior portion before they are pushed laterally by the reproductive organs.

Close to, and intermingling with, the inner longitudinal muscles are fibers from the dorso-ventral and lateral systems. These fibers, as the name implies, extend from the dorsal to the ventral surfaces of the basement membrane in which they are embedded. The lateral fibers are similarly arranged. Some of these fibers in passing the inner longitudinal muscles give off branches to this system and a few may be found extending at right angles to the inner longitudinal mass as circular muscles. This is not typical except in the middle of the body where these fibers form a layer of circular muscles lying close to those of the inner longitudinal system. The muscles passing through the inner muscle mass divide when they come within a few micra of the longitudinal muscles in order to pass between them to their insertions on the basement membrane.

Specialized muscles are also present. In the scolex the longitudinal cuticular muscles become specialized and aid in the retention of the shape of the scolex. These muscles are particularly plentiful in the loculi where they extend from the basement membrane of one across to a similar position on the loculus directly opposite (Fig. 19). A few of these fibers are also encountered in the ridges between the loculi, although the bulk of the musculature of these may be traced to the inner longitudinal muscles. These have been described in detail in the portion of this paper treating the scolex. Other specialized muscles occur in the usual portions of the reproductive system and a detailed account of them will be found in the later paragraphs.

The excretory system of *G. hexacotyle* is typical of this group of Cestodaria. There is a series of main ascending and descending canals; smaller canaliculi go to form the main ascending ducts and these canaliculi are in turn formed by the renal corpuscles or flame cells. In the scolex the ascending canals break up only to form the descending canals.

The main descending canals enter an excretory bladder or vesicle in the posterior part of the body behind the post-ovarian vitellaria. The canals enter the vesicle from all sides near the anterior lateral portion. At this point, which is the widest of the bladder, the vesicle measures 48 by 24  $\mu$ . As the exterior is approached the cavity becomes narrower until it is only 19 by 14  $\mu$  or less. This excretory bladder may therefore be described as pyriform. The length of this vesicle is between 45 and 55  $\mu$ . The bladder is surrounded also by cuticular muscles and this fact demonstrates that it is not a true pulsating excretory vessel as one finds in the trematodes.



The material is in such poor condition that no attempt will be made to work out the nervous system. Two lateral nerves show in cross section in the base of the scolex.

The male reproductive system is typical of the Caryophyllaeinae and is confined to the medullary parenchyma throughout. The various components of the system will be considered in their natural sequence. The testes are large and numerous and are confined to the field between the rows of vitellaria which in this species are entirely lateral. As might be expected the inner longitudinal muscles surround the vitellaria and the testes. In cross section these glands are flattened somewhat dorso-ventrally, and are present in 2 dorsal and 2 ventral rows, although anteriorly there are 3 rows. In size they measure between 0.144 and 0.264 mm. long, and 0.072 to 0.199 mm. wide, and number in the adult between 175 and 200 (Fig. 42). This figure was checked by an estimation of the number of testes present followed by an actual count.

The vas deferens is indistinguishable in the most anterior portions of the parasite. It first appears about one-half the distance to the cirrus sac as a small winding duct lying in the center of the medullary parenchyma. This gradually increases in size until the vas deferens becomes gorged with spermatozoa. About this time the testes disappear, first the median ones and later those on the side, leaving the entire medullary field, with the exception of the vitellaria at the lateral margins, to the coils of the vas deferens which become more dilated posteriorly. These reach a maximum diameter varying between 36 and 50  $\mu$ , although the latter figure is more typical. After numerous convolutions this structure approaches the median dorsal surface. Here it passes into the narrow, muscular ductus ejaculatorius, which continues in a posterior direction. Shortly this duct expands into an enlarged portion, the seminal vesicle. This structure is prominent and well set off from the remainder of the duct. The vessel is lined with a cuticula-like substance and this is surrounded by a layer of circular muscles intermingled with a few longitudinal fibers. The seminal vesicle narrows, dips ventrally and passes into the cirrus sac. The total length of the ductus ejaculatorius including the seminal vesicle is about 0.21 mm. The vesicle has a maximum length of 0.19 mm. and a width of 0.96 mm. and the cavity ranges between 0.146 and 0.156 mm. by 0.048 to 0.060 mm. The circular muscles form a layer which varies from 9 to 24  $\mu$  in thickness. The measurements include the young adults, for both young and old sexually mature material was studied.

The nearly round, prominent cirrus sac lies on the ventral surface directly beneath the ductus ejaculatorius and seminal vesicle, and occupies about one half the medullary parenchyma. The ductus ejaculatorius enters from the median dorsal surface. The cirrus sac has a maximum diameter of about 0.228 mm. The younger adults had cirrus sacs which measured

only 0.168 mm., even though the worms were fully developed and sexually mature. However, the thickness of the musculature was identical in both cases and measured between 14 and 26  $\mu$ . The cirrus was not extruded but the canals of the cirrus sac were evident as was the serrated inner canal of the retracted cirrus (Fig. 41). The cirrus sac opens flush with the ventral surface of the parasite, and the female system empties in a similar fashion just behind that of the male.

The vitellaria are unusual because they do not completely surround the testes, but instead lie in two lateral fields with the testes between. The inner longitudinal muscles extend about the testes and vitellaria (as in other members of the Caryophyllaeinae). The two lateral fields extend posteriorly until nearly opposite the cirrus sac. There is also a group of post-ovarian vitellaria which lie between the oötype and the excretory vesicle. These glands have a maximum diameter of 0.21 mm. The vitelline ducts from the anterior vitellaria run posteriorly through the medullary parenchyma. After the cirrus sac is passed these ducts run laterally and then medianly by the ovary so that they pass on the inner side of it. These canals swell lightly to form vitelline reservoirs and then dip ventrally, first uniting, and passing under the ovarian commissure. Here it is joined by the single vitelline duct from the post-ovarian vitellaria. This canal arises from the central portion, passes anteriorly and to the left, dipping ventrally to join the single main vitelline duct from the anterior. This single vitelline duct empties into the fertilization chamber, or vaginal-oviduct canal, just behind the juncture of the oviduct with the vagina (Fig. 41).

The ovary is lobate, "H" shaped and possesses no unusual characteristics. The main limbs of the ovary measure between 0.8 and 0.9 mm. in length by 0.096 to 0.122 mm. in width. The ovarian commissure instead of extending straight across from one wing to the other is "V" shaped, with the apex of the "V" posterior. The median portion of the commissure forms a fairly distinct ovarian reservoir which measures about 0.21 by 0.14 mm. The poorly defined oöcapt extends 10  $\mu$  from the ventral surface of the reservoir and measures from 12 to 15  $\mu$  in diameter to about 10 to 11  $\mu$  in length. The muscles are not as clearly marked as in other species. The remainder of the canal is the oviduct and is less than 15  $\mu$  in length.

The female genital atrium lies behind the cirrus sac of the male system. It follows the curves of the cirrus sac from its most posterior position, ventrally and anteriorly until it opens on the surface 20 to 26  $\mu$  behind that of the male. The total length of this duct from its most dorsal portion, which is the beginning of the vagina, to the surface, varies between 0.24 and 0.26 mm. The uterus empties into the female cloaca from the right side, 0.16 to 0.19 mm. from the distal end of the atrium. The

female cloaca continues dorsally from the point of entrance of the uterus for nearly 0.07 mm. before it turns posteriorly to form the vagina.

The vagina in this species winds posteriorly making numerous convolutions, the majority of which are in a dorsal-ventral direction. As the ovarian commissure is reached the canal passes dorsally to a position above it. Here the vagina becomes enlarged to form a small but distinct receptaculum seminis measuring about 60 by 24  $\mu$  in cross section. Upon resuming its normal size, a diameter of less than 20  $\mu$ , the vagina comes to lie close to the walls of the ovarian reservoir. It is now surrounded by a cellular layer in which are found circular muscles. The duct passes ventrally near the posterior edge of this structure until close to the ventral surface where it doubles back upon itself to join the oviduct. The entire length of the oviduct, including the oöcapt, is between 25 and 30  $\mu$  (Fig. 84). The combined oviducal-vaginal canal forms the fertilization chamber which passes dorsally and then sweeps posteriorly in a semi-circle where the common vitelline duct joins the fertilization chamber to form the uterus. The oötype surrounds the aforementioned structures.

The convoluted uterus leads posteriorly where the thin walled portion of the egg filled uterus is found. The characteristic uterine glands do not appear until the main ascending limb is opposite the posterior portion of the ovary. Here the unicellular uterine glands appear and the uterus winds medianly and dorsally over the ovarian commissure whereupon the typical coils and convolutions form. These now extend anteriorly to the cirrus sac, and empty as already described into the female cloaca (Fig. 41). The eggs of this species are ovoid and measure between 37 and 41  $\mu$  in length by 23 to 30  $\mu$  in width. The shell is about 1  $\mu$  in thickness and appears non-operculate.

*Glaridacris hexacotyle* was the second species to be described from North America. Linton (1897) placed this parasite in the genus *Monobothrium*. It clearly belongs in the Caryophyllaeidae and falls into the Caryophyllaeinae on the basis of the medullary vitellaria surrounded by the inner longitudinal muscles. Because of the three loculi on the scolex and the presence of an external seminal vesicle this form is barred from the genus *Caryophyllaeus*. Furthermore in the latter genus the vitellaria are arranged annularly and in *G. hexacotyle* they are confined to the more lateral portions of the medullary parenchyma. *G. hexacotyle* differs from the genus *Monobothrium* in the type of genital atrium and the scolex which normally possesses the hexagonal shape and the characteristic introvert. In respect to the character of the three pairs of loculi it resembles the genus, *Hypocaryophyllaeus*, but in this genus the uterine coils are anterior to the cirrus sac and occupy only one fourth or less of the space taken by the testes. It therefore cannot be placed there. The possession of the three loculi places it in the genus *Glaridacris* which is characterized by the possession of three



pairs of loculi or bothria. The type of genital atrium, ovary, position of uterine coils, presence of post-ovarian vitellaria and external seminal vesicle clearly mark it as belonging to this genus.

In the genus *Glaridacris* there are two other species, both from the same host, *Catostomus*. The scolex of *G. laruei* is of the "Π" type, while the scolices of *G. catostomi* and *G. hexacotyle* are very similar, except that the latter is typically conical while the former is broader at the tip and does not have the loculi uniting to form a conical apex. The cuticula of *G. catostomi* is two to three times as thick as that found in *G. laruei* and *G. hexacotyle*, and the number of testes clearly sets this latter species off from the others as does the anterior vitellaria which are arranged in two distinct un-united lateral fields. In *G. catostomi* the cirrus sac occupies all the medullary parenchyma compared with one-half the medullary parenchyma in *G. hexacotyle*; in the former cirrus sac muscles have a diameter of 43 to 48  $\mu$  while those of *G. laruei* and *G. hexacotyle* measure respectively 16 to 21  $\mu$  and 14 to 26  $\mu$ . These two are alike in that a common genital atrium is lacking or inconspicuous while the female atrium lies respectively 11 to 19  $\mu$  and 20 to 26  $\mu$  posterior to that of the male. Two of these species, *G. hexacotyle* and *G. laruei* form distinct seminal receptacles in the posterior portion of the vagina. The ovaries vary somewhat in maximum length, as do the ovarian commissures. Perhaps the most significant difference is the "V" shaped ovarian commissure found in *G. hexacotyle*. The oöcapit, diameter of the ovarian commissure, and length of the oviduct all constitute differences of minor importance, while the peculiar lateral position of the vitellaria in *G. hexacotyle* as compared with the arrangement in other species is of greater import. Also in all species of this genus except *G. hexacotyle* the expanded common vitelline duct forms the reservoir. However in this latter species the several vitelline ducts expand and serve as reservoirs for the vitelline material. Lest it be argued that such a condition would occur normally let me call attention to the fact that these ducts are usually small, 10 to 15  $\mu$  or less in diameter, and are not possessed of walls that would permit expansion to a vitelline receptacle measuring four or five times as great. The eggs of *G. laruei* and *G. hexacotyle* are closely allied and measure 39 to 42  $\mu$  by 26 to 30  $\mu$  and 37 to 41  $\mu$  by 23 to 30  $\mu$  respectively. *G. catostomi* has eggs which measure 54 to 60  $\mu$  by 38 to 48  $\mu$ . The type of matrix found in the medullary parenchyma is also peculiar to *G. hexacotyle* alone. These differences serve to show beyond question the validity of this species.

*GLARIDACRIS LARUEI* (LAMONT 1921)

[Figs. 4, 36, 49, 50, 78]

1921: *Caryophyllaeus laruei*

1924: *Caryophyllaeus laruei*

1927: *Glaridacris laruei*

Lamont 1921: 1- 4

Johnston 1924: 347

Hunter 1927: 20-21

Specific diagnosis: With the characters of the genus. Adults up to 9.5 mm. long by 0.95 mm. wide. Parasite characterized by prominent scolex about 0.4 mm. long, bearing 6 loculi and terminal disc, forming the "II" type. Disc measures about 0.06 mm. in thickness and scolex has maximum width below terminal disc of 0.55 mm. Neck distinct, having a maximum width of 0.96 mm. Body oval to cylindrical in cross section, not readily separated into subcuticula and cortical parenchyma which together measure 40 to 55  $\mu$  in thickness. Both inner and outer longitudinal muscles present, latter only indistinctly in neck region. Testes irregularly ellipsoidal, numbering between 60 and 85, 0.12 to 0.18 mm. in maximum diameter. Cirrus sac small, circular occupying about one-half of medullary parenchyma. It has a diameter of 0.108 to 0.120 mm. and the circular muscles vary between 16 and 21  $\mu$  in thickness. True genital atrium is absent and reproductive systems open on the ventral surface 12 to 19  $\mu$  behind each other. Vagina median, ventral, moderately convoluted and forms a distinct receptaculum seminis which measures 0.096 by 0.072 mm. Wings of ovary are 0.5 to 0.7 mm. long and 0.05 to 0.55 mm. wide. Vitellaria do not completely surround testes and have maximum diameter of 0.1 to 0.2 mm. by 0.03 to 0.05 mm. Excretory system composed of 8 pairs of excretory canals and terminal excretory vesicle measures 45 by 24  $\mu$ . Eggs ovoid, non-operculate and measure 39 to 42  $\mu$  by 26 to 30  $\mu$ .

Host: *Catostomus commersonii*, Green Lake and Lake Mendota, Wisconsin; Douglas Lake, Michigan. In intestine.

Type: Slide No. 197 in Museum of Zoology, University of Michigan, Ann Arbor, Mich.

Paratype: Slide No. 13.16 in the collection of Dr. Henry B. Ward.

Host	Locality	Collector	Authority
<i>Catostomus commersonii</i> (Lacépède)	Green Lake and Lake Mendota, Wis.	A. S. Pearse	Lamont 1921: 1-4 Hunter (the present paper)
<i>Catostomus commersonii</i> (Lacépède)	Douglas Lake, Mich.	G. R. La Rue	Hunter (the present paper)
<i>Catostomus commersonii</i> (Lacépède)	Douglas Lake, Mich.	A. R. Cooper	Hunter (the present paper)

This species was imperfectly described by Miss Lamont (1921). Through the kindness of the University of Michigan Museum it was possible to obtain the original type specimen for comparison and study. This was the



only material which they had, and it was not in the best state of preservation. The same species, however, was obtained from *Catostomus commersonii* taken from Douglas Lake, Michigan by both Drs. G. R. LaRue and A. C. Cooper, and this material furnished ample specimens so that the description could be completed. Lamont (1921) secured her material from *Catostomus commersonii* taken from Green Lake, Wisc. She states that one specimen contained 24 individuals of this species and that two of the suckers from Lake Mendota, Wis. were also infected with this parasite.

The body of this parasite measures between 5.2 and 9.5 mm. in length and possesses a maximum width of 0.85 mm. The worm is flattened dorso-ventrally and shows but slight changes in width. The vitellaria are confined to the more lateral portions the testes lying median to them. In the posterior fifth of the body is found a part of the male and the female reproductive system. In a specimen measuring 5.2 mm. in length, the type of "*C. laruei*", the maximum width was 0.73 mm. and the distance from the tip of the scolex to the first vitellarium was 0.96 mm. The neck measured only 0.42 mm. in width. Posteriorly the body widens slightly until just before the region of the cirrus sac, where it narrows to about 0.6 mm. and behind the sac the body width drops to 0.5 mm. and then tapers posteriorly to the distal end of the body. Measurements of other specimens of this species show that these figures are typical. The table gives the maximum and minimum encountered in a study of fifteen specimens.

Length.....	4.2	-9.5	mm.
Maximum width.....	0.5	-0.95	
Width of neck.....	0.4	-0.55	
Width of body anterior to cirrus sac.....	0.5	-0.6	
Width of body posterior to cirrus sac.....	0.45	-0.55	
Maximum width of scolex.....	0.5	-0.6	
Maximum length of scolex.....	0.3	-0.75	
Width of base of scolex.....	0.45	-0.59	
Thickness of terminal disc of scolex.....	0.058	-0.065	

The scolex is a well defined structure and appears to be characteristic for the species. The base is considerably wider than the apex, which is a flattened disc. This disc measures about 0.06 mm. in thickness and may be elevated or depressed. Beneath the disc are the irregularly marked loculi, called "poorly defined suckers" in the original paper. There are 6 loculi present. The inner longitudinal muscles extend anteriorly into the scolex and are inserted on the lateral portions of the terminal disc, thereby forming with the disc the Greek letter " $\Pi$ " so evident in toto mounts. The maximum width of the scolex is below the terminal disc which measures about 0.55 mm. (Fig. 4).

The cuticula is narrow and measures between 2 and 3  $\mu$  in thickness. It

is bounded internally by a very thin basement membrane which is less than  $1\ \mu$  thick. Beneath this lie the characteristic circular and the longitudinal cuticular muscles. The former lie beneath the basement membrane and the latter are scattered in bundles close to the circular layer. One or two are grouped together in a bundle.

The musculature of this species is quite typical of the Caryophyllaeinae and is composed of inner and outer longitudinal muscles. The fibers of the outer longitudinal muscle system are infrequently found in the neck region where they lie 7 to  $10\ \mu$  under the basement membrane. In the more posterior parts of the body this outer layer becomes lost. The distinct muscles of the inner longitudinal system are found 40 to  $64\ \mu$  from the cuticula separating the cortical and the medullary parenchyma. Beneath this muscle layer lie the vitellaria which are arranged annularly about the testes. More than 10 individual muscles are found in each fasciculus which in frontal sections lie so close to each other as to form a muscular sheet. In the posterior region the muscles of the inner longitudinal system are pushed towards the surface by the distended organs of the reproductive systems notably the uterine coils.

Special musculature was apparent only in the case of the cirrus sac, seminal vesicle and ductus ejaculatorius in the male system. The cirrus sac muscles measured 16 to  $21\ \mu$  in thickness while those of the seminal vesicle were only 10 to  $12\ \mu$ . The walls of the ductus ejaculatorius were surrounded with a thin layer of circular muscles. Those of the other regions will be described as they are encountered.

The excretory system shows 8 pairs of canals, ascending and descending. The latter are more median and the former are composed of numerous smaller canaliculi which in turn doubtless take their origin from renal corpuscles or true flame cells, depending upon the type present. Anteriorly the canals of the ascending system send a few canals into the scolex which do not anastomose freely but turn posteriorly to form the descending canals which empty into the excretory vesicle at the posterior tip of the body. This vesicle is surrounded by deep staining myoblastic cells. Some of the fibers of the inner longitudinal muscles are embedded in the walls of this vesicle. This bladder measures about 45 by  $24\ \mu$ ; the canals of the excretory system empty radially at its anterior end. The vesicle opens posteriorly and ventrally.

The testes are usually arranged in two rows, although sometimes only one is found and occasionally there will be three rows. In such cases the third is ventral to the other two. These glands are surrounded laterally by the vitellaria, which usually extend well over the dorsal and ventral surfaces nearly enclosing the testes in a ring. The long axis of each testes is generally lateral, though some lie in an anterior-posterior plane. There are about 70 testes in an adult. This number when checked by actual count

and the system of estimation outlined on page 11, showed that the range is between 60 and 85. In shape these glands are globular and lobate their size ranging between 0.12 and 0.18 mm. in length and 0.072 to 0.12 mm. in width. The average length based upon the measurements of 25 testes is 0.146 mm. and the average width is 0.085 mm. (Fig. 49). The convoluted vas deferens becomes visible in between the two rows of testes in the last two fifths of the body, the testes ending nearly 0.2 mm. anterior to the cirrus sac. It was noted that although the loosely coiled vas deferens was filled with spermatozoa it was not distended. It has a maximum diameter of 25 to 30  $\mu$  and is confined to the ventral portions of the medullary parenchyma. After making several convolutions it passes ventrally and empties into the narrow muscular ejaculatorius at the seminal vesicle (Fig. 36). The seminal vesicle is relatively small and was mistaken for the cirrus by the original describer. This statement is based on the structure labelled "cirrus" on the original plate which has the same position and shape as the combined seminal vesicle and ductus ejaculatorius. As in the case of other seminal vesicles the cavity is lined with a smooth membrane about which lie the circular muscles; these measure 12 to 14  $\mu$  in thickness. This vesicle has a length of 0.079 mm. and a width of 0.048 mm. The ductus ejaculatorius leaves dorsally and is about 60  $\mu$  in length emptying into the cirrus sac from the anterior dorsal surface. It is lined throughout with circular muscles of the same thickness as those surrounding the seminal vesicle. This marks the duct as unusual, for it is more typical to find the musculature of the canal thinner than the layer about the seminal vesicle. Furthermore, the ductus ejaculatorius is long, for it measures between 130 to 140  $\mu$  in total length after leaving the seminal vesicle, and extends for 10 to 15  $\mu$  from the anterior side of the vesicle (Fig. 36). The cirrus sac lies near the ventral surface and appears somewhat ovoid measuring about 0.108 mm. in width and 0.12 mm. in greatest diameter. This difference is probably due to the pressure of the cover slip in the toto mount, for in sectioned material the vesicle appeared nearly round. The musculature varies between 16 and 21  $\mu$  in thickness. The cirrus occupied the lower half of the cirrus sac and a few retractile muscle fibers extending from the distal wall of the sac to parts of the cirrus. The cirrus does not open into an atrium, but instead it opens even with the surface about 12 to 19  $\mu$  anterior to a similar pore of the female reproductive system (Fig. 50).

The ovary is lobate and measures between 0.5 and 0.6 mm. in length and between 0.5 and 0.55 mm. in width. The ovarian commissure connecting the two arms of the ovary tapers towards the center. At this point it measures 0.05 to 0.07 mm. wide; it is 0.3 mm. from the posterior edge of the cirrus sac. The main arms of the ovary extend anteriorly as far as the posterior edge of the cirrus sac where they are nearly joined by the lateral portions of the vitellaria from the anterior part of the body.



The vitellaria lie in two lateral fields several layers deep. In the younger specimens these do not extend over the dorso-ventral surfaces to any marked degree, but in individuals over 2 mm. in length they spread out to make a ring about the testes. They are roughly rectangular in shape and measure between 0.1 and 0.2 mm. in length and 0.03 to 0.05 mm. in width. The vitellaria do not mingle with the testes, but are confined laterally about them. They are slightly more numerous in the posterior regions of the body. There is a third group, the post-ovarian vitellaria, which are found between the posterior coils of the uterus and the excretory vesicle. The vitelline ducts first appear anterior to the cirrus sac; they pass posteriorly on the inner side of the ovary and then unite to form the single vitelline duct. This canal expands distally to serve as the vitelline reservoir. It passes dorsally to the ovarian commissure and then dips ventrally into the ovarian complex where it soon joins the vaginal-oviducal canal, first connecting with a single duct from the post-ovarian vitellaria (Fig. 36).

The vagina runs posteriorly from the female cloaca and the uterus enters from the left side, 0.07 mm. from the posterior margin of the cirrus sac. The cloaca is 0.048 to 0.055 mm. in width at this point and maintains the same width until it narrows near the cirrus sac. Shortly after the vagina leaves the cloaca it turns ventrally and gives way dorsally to a large receptaculum seminis approximately 0.096 mm. long by 0.072 mm. wide. The vagina then passes posteriorly and dorsally to the ovarian commissure. It follows close to the ovarian commissure and passes ventrally to enter the ovarian complex.

The oöcapt arises from the median posterior edge of the ovarian commissure and winds its way laterally into the oötype complex. The sphincter muscle controlling the release of the ova is about 6 to 8  $\mu$  thick, and the total diameter of this tube and muscular wall is between 10 and 13  $\mu$ . It extends posteriorly for 10  $\mu$  before it gives rise to the less muscular oviduct which unites with the vagina to form the oviducal-vaginal canal, or fertilization chamber. Less than 7  $\mu$  from the juncture of these two canals the vitelline duct unites to form the uterus (Figs. 36, 50). The uterus coils through the small oötype and then passes posteriorly. The uterus is thin walled until the anterior limb of the uterus is opposite the posterior arm of the ovary. At this point the unicellular uterine glands appear and completely surround the uterus. The function of these cells is not known. The convolutions of the uterus do not pass anteriorly to the cirrus sac and after several twists empties into the female genital atrium from the left side. The uterus was filled with eggs, some of which retained their original shape. These were non-operculate and possessed a moderately thin shell beneath which were heavy enveloping membranes. The eggs were small, nearly oval and measured between 39 and 43  $\mu$  in length and 25 and 31  $\mu$

in width. The average size based upon 20 eggs was  $40.9\ \mu$  by  $28.95\ \mu$ .

The material which furnished the basis for the original description of this parasite was secured from *Catostomus commersonii*, Lacépède, taken from Lake Mendota, Wisconsin on August 22, 1919 and Green Lake, Wisconsin on August 25, 1919. Miss Marion E. Lamont described this helminth. The description was extremely inadequate as she was apparently unaware of the existence of papers already published in this country, notably that of Cooper (1920) and those of Linton (1893, 1897).

Sometime later some Cestodaria from *C. commersonii* also taken from Lake Mendota were sent to Dr. Cooper for identification. He determined them as being *G. catostomi* which he had described in 1920. A careful study of Cooper's material and the type specimen of "*G.*" *laruei* from the University of Michigan Museum, as well as the slides sent to Dr. Cooper for identification by Dr. Pearse, shows that "*C.*" *laurei* and *G. catostomi* are not identical. In order to ascertain this beyond question the author went to Lake Mendota, Madison, Wisconsin to secure additional material. But even though Professor M. F. Guyer was extremely kind and other members of the staff furnished nets, etc. it was impossible to secure any more infected fish. Fortunately, however, Cestodaria belonging to this species were subsequently found in collections of Drs. G. R. LaRue and A. R. Cooper from Douglas Lake, Michigan which enabled me to ascertain the validity of the species.

This species readily falls in the Caryophyllaeinae and by virtue of the type of scolex may be placed in the genus Glaridacris. The scolex characteristic for this species has been described as the "II" type and differs from *G. hexacotyle* in not being pointed distally and from *G. catostomi* in not being wedge shaped. Both lack the terminal disc so characteristic of this species. It resembles *G. hexacotyle* and *G. catostomi* in the possession of 6 rather than 4 loculi as recorded by Lamont (1921:2). The matter of this type of scolex will be considered in detail later. The cuticula of *G. laruei* measures between 2 and  $3\ \mu$  in thickness and this is thinner than that found in any of the other species, for *G. hexacotyle* and *G. catostomi* have a cuticula measuring 3 to 5 and 7 to  $11\ \mu$  respectively. That this layer of *G. laruei* is simply thinner because it is younger may be answered by pointing to the larvae of *G. catostomi* where the cuticula was found to be about  $25\ \mu$  in thickness. In other words the thickness of the cuticula, at least in *G. catostomi*, appears to be inversely proportional to its age and size. The outer longitudinal muscles are not as distinct as in *G. catostomi* where they stand out with great clarity. In fact in many of these species the outer longitudinal muscles are so poorly developed as to be almost absent. The testes in *G. laruei* number between 60 and 85 as compared with 175 to 200 and 405 to 420 for *G. hexacotyle* and *G. catostomi*. These glands are completely surrounded by the vitellaria in all



cases except *G. hexacotyle* where they are confined anteriorly to two lateral rows and *G. laruei* in which the vitellaria nearly surround them. In the latter species the cirrus sac is small, circular, occupying only one half of the medulla and has a maximum diameter of 0.108 to 0.120 mm., the smallest yet recorded. In *G. laruei* the male and female reproductive systems do not open into a common genital atrium, but instead open even with the surface behind one another. In contrast to this condition is *G. hexacotyle* with an atrium of 3 to 5  $\mu$  in depth and *G. catostomi* whose common genital atrium measures between 0.7 and 0.15 mm. in depth. The female reproductive systems open 12 to 19  $\mu$  posterior to that of the male in *G. laruei*. In all the other members of this genus this distance is vastly greater, with the exception of *G. hexacotyle* in which the distance is 20 to 26  $\mu$ . Once more *G. catostomi* may be separated from *G. laruei* on the basis of size of eggs, for in this species they are 15 to 20  $\mu$  larger than those of *G. laruei*. The latter, however, has the same size eggs as *G. hexacotyle*, measuring respectively 37 to 42 by 23 to 30  $\mu$ . One difference, however, is apparent, for the embryos of *G. laruei* are surrounded by a thin outer shell under which lies a heavy enveloping membrane not found in the eggs of *G. hexacotyle*. Furthermore, this latter species possesses a characteristic type of parenchyma which differs from anything yet encountered.

Cooper (1920) confused specimens of *G. laruei* and *G. catostomi* (a full discussion of this occurs on page 59). It is also evident that scolices of this parasite may take several different shapes. The typical example shows the terminal disc well protruded with the three loculi situated in between the so-called "II." How this disc becomes extruded is an interesting study, but some light is thrown on the problem from the data at hand. In the case of specimens with fully contracted scolices the terminal disc alone shows. The remainder of the scolex appears swollen laterally and microscopic examination reveals the presence of the parallel longitudinal muscles within the scolex drawn down inside by the action of the strong inner longitudinal muscles. Rarely the terminal disc is absent, evidently having disappeared by being pulled in between the bands or due to degeneration of the scolex before fixation. The former condition is indicated by 2 small humps extending distally from the rounded portion of the scolex. In such cases the width of the organ is decreased; the muscle bands are evident at this stage also. By the contraction of the muscles in the base of the scolex the circumference is decreased. Since the body cannot increase materially in width, this protoplasm, including the liquids in the excretory canals are forced into the distal portion of the scolex. In other words it is forced *between* the inner longitudinal muscle bands which form the two protrusions. Then by the action of specialized muscles the distal end flattens out and forms the terminal disc giving the typical "II" shaped scolex which is so characteristic of this species. This

species differs from *Glaridacris confusus*, in several important respects, but likewise has some characteristics in common. Thus the adults are about the same length and typically possess the same type of scolex; furthermore the cuticula is essentially the same, and in both parasites the subcuticula and cortical parenchyma is combined in one. This layer is 15 to 40  $\mu$  in thickness in *G. confusus* compared with 40 to 55  $\mu$  in *G. laruei*. The testes number 60 to 85 in the latter and only 25 to 35 in the former, while the muscles of the cirrus sac measure respectively 16 to 21  $\mu$  and 10 to 17  $\mu$ . In both cases the reproductive systems open on the surface, the male and female pores being only 12 to 19  $\mu$  apart in *G. laruei* compared with 20 to 55  $\mu$  in *G. confusus*. In the former the vitellaria nearly surround the testes while in the new species they are confined to two lateral rows as in *G. hexacotyle*. And lastly the hosts are very different for *G. laruei* is reported only in *C. commersonii* while the latter was taken from *Ictiobus bubalus*, *Ictiobus* sp. and *Dorosoma cepedianum*.

*GLARIDACRIS CONFUSUS* HUNTER 1929

[Figs. 22, 24, 43, 66-68]

1929: *Glaridacris confusus*

Hunter 1929: 189-190

Specific diagnosis: With the characters of the genus. Adults usually 3 to 7 by 0.2 to 0.8 mm., flattened dorso-ventrally. Scolex oval at base, tapers to a chisel-shaped extremity which is cut by 6 loculi. Inner longitudinal muscles are usually present drawn into four prominent and four weaker groups of fasciculi confined to lateral thirds of base of scolex; outer longitudinal muscles rudimentary. Cuticula 2 to 4  $\mu$  thick. Subcuticula inseparable from cortical parenchyma combined width of 15 to 40  $\mu$  except in neck and scolex. Medullary parenchyma occupies three fourths of body width. Testes large, 0.1 to 0.3 mm. by 0.1 to 0.13 mm. and numbering 25 to 35; they occupy two parallel rows. Cirrus sac fills one third to one half medullary parenchyma, maximum diameter 0.16 mm.; circular muscles 10 to 17  $\mu$  thick. Male and female reproductive systems open on surface 20 to 55  $\mu$  apart. Vagina forms large receptaculum seminis, "S" shaped and situated anterior and dorsal to ovarian commissure which are 0.13 to 0.27 mm. long and 0.031 to 0.067 mm. wide. Vitellaria confined to two lateral rows, 0.067 to 0.135 mm. maximum diameter. Eggs small, ovoid, 37 to 48 by 20 to 31  $\mu$ .

Host: *Ictiobus bubalus*, Rock River, Illinois and Mississippi River, Fairport, Iowa; *Ictiobus bubalus*, *Ictiobus* sp. and *Dorosoma cepedianum*, Tallahatchie River, Mississippi. In intestine.

Type: Slide No. 29.41 in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota.

## Material in author's collection No. 642.2-642.10.

Host	Locality	Collector	Authority
<i>Ictiobus</i> sp.	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
<i>Ictiobus bubalus</i> (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
<i>Ictiobus bubalus</i> (Rafinesque)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)
<i>Ictiobus bubalus</i> (Rafinesque)	Mississippi River, Fairport, Ia.	—	Hunter (the present paper)
<i>Dorosoma cepedianum</i> (Le Sueur)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)

The material forming the basis of this description was taken by Dr. Parke H. Simer in Mississippi during the spring of 1927. In many cases the tissues appeared somewhat vacuolated. According to Dr. Simer's report he used Bouin's picro-formol-acetic or a saturated aqueous solution of mercuric chloride. Both of these fixatives should give excellent results. The reason for this supposedly poor fixation can be traced to the hosts which undoubtedly had to lie out of water exposed to the warm air for hours before they were examined. Cestodaria are particularly sensitive to such exposure and if they do not leave the host will soon decompose. It has been observed by the author that the scolex is the first region to become affected. This accounts for the apparently great diversity of shapes assumed by the scolex within the confines of a single species. Such differences do not occur in the living material and this forms one of the greatest arguments for the use and study of living specimens. The exact nature of this effect cannot be stated; whether the digestive juices which are released in quantity as the fish dies have a deleterious action upon the portion of the parasite in contact with the host, or whether the reproductive system is more resistant is not apparent. The result in either case is the same. In describing this and other species the author has endeavored to use specimens which have not undergone this degeneration.



Figure 22 shows the most common type of scolex encountered, although many variations were met.

*Glaridacris confusus* is relatively small, and broad. The adults when fixed measure between 3 and 7 mm. Occasionally specimens were found which measured nearly 20 mm. These all were fully matured forms as was evidenced by the presence of great numbers of eggs in the uteri. In many instances the parasites were contracted due to the action of the well developed inner longitudinal muscles. Such contraction tends to increase the breadth which varied between 0.27 and 0.8 mm. Maximum breadth occurs at the base of the scolex (Fig. 22). This organ is oval at the base, and tapers to a chisel-shaped extremity which is cut by six loculi (Figs. 66, 67). The region of the cirrus sac and uterine coils was the next widest place while the short neck universally constituted the narrowest. This latter region is hardly discernible for it gives way immediately to the body which contains the reproductive organs. Upon examining a toto from the ventral surface one is impressed by the compactness of the uterine coils which do not extend beyond the anterior limits of the cirrus sac (Fig. 24).

There are several other rather striking features characteristic of this species. The cuticula while very thin, measuring between 2 and 4  $\mu$ , is subdivided into several parts or regions. The outermost strip takes the stain less deeply than the inner and thicker portion. In some cases slight vacuolization occurred, but in these one also found a scolex undergoing degeneration. This evidence supports the conjectures made by the author in regards to the fixation of *C. terebrans* and other species. In cases of vacuolization the cuticula appeared slightly thicker, but in normal specimens the cuticula never exceeded 4  $\mu$ . It was thinner upon the scolex than in other parts of the body. The inner layer of the cuticula constitutes two thirds of the whole and takes the counter stain deeply. Beneath this and usually in contact with it, replacing the customary basement membrane, lies the thin layer of circular cuticular muscles. This is followed by the bands of longitudinal muscles. Each occupies less than 1  $\mu$ . Apparently the subcuticular layer and the cortical layer of the parenchyma have become fused into a single undivided mass. This was also the case with *G. hexacotyle*. The outer longitudinal muscles appear to degenerate for in many cases they could not be found. There is some reason to believe they may have become fused with the longitudinal cuticular muscles for some times a second mass of fibers could be discerned only a few micra from the cuticular layer. These are thought to be the remains of the outer longitudinal muscles which have degenerated. This combined subcuticula and cortical parenchymal layer is narrow and measures but 15 to 40  $\mu$  in all parts of the body except the neck and scolex where it may be 60  $\mu$ . Scattered throughout the body are a few dorso-ventral muscle fibers taking their ori-

gin from the inner longitudinal muscles. These fibers are more prominent in the region of the reproductive system (Fig. 43).

In studying a toto mount one is inclined to place the specimen amongst the Lytocestinae due to the inner longitudinal muscles. As these leave the scolex one sees in a dorsal or ventral view four rows of muscles, two on each side; the more median ones appear to run between the testes and the vitellaria (Fig. 24). A closer examination shows the spreading of these fibers into a sheet which surround the vitellaria and testes. An examination of cross sections dispels any doubts as to the disposition of these muscle layers and one is forced to the conclusion that it belongs in the Caryophyllaeinae (Fig. 68). The excretory system is characteristic of the group and presents no unusual features. In the scolex are only a few branches of the system and as the neck is reached these assume a more orderly arrangement. The number of pairs of ascending and descending canals varies but are between ten and twelve. They appear in the combined subcuticular and cortical parenchymal layer. Posteriorly they pass into a terminal pear-shaped excretory vesicle which ranges in size from 0.11 to 0.13 mm. by 0.020 to 0.030 mm. the ducts emptying into the vesicle at its widest point. It is lined with a continuation of the cuticula. Little could be seen of the nervous system except the two ganglia in the base of the scolex (Fig. 22).

The outstanding feature of the male reproductive system is the small and constant number of testes, which range between 25 and 35. They are nearly round and are packed closely together, being much larger in proportion than the vitellaria which are confined to two lateral fields. The testes measure 0.1 to 0.3 by 0.1 to 0.13 mm. and in toto mounts appear granular, taking the haematoxylin stain as deeply as the ovary. In section they appear to be composed of a number of small globes, the margins of which are lined with cells. Thus there are a quantity of small circles, whose outlines appear stippled, going to make up the true testes (cf. *Monobothrium ingens*). These are perhaps the seminiferous tubules. The vas deferens appears about the middle of the testicular field and as the last testis is passed it fills the entire medullary field with its convolutions. After a number of lateral twists first to one side and then to the other the vas deferens narrows and assumes a median position and wanders towards the cirrus sac. It is, however, dorsal and anterior to it. Less than 0.1 mm. from the cirrus sac it dips ventrally and anteriorly passing into the muscular seminal vesicle. This structure is a large crescent shaped organ, with one end lying beneath and to the right of the cirrus sac and the other entering this organ by means of the ductus ejaculatorius on its anterior median dorsal surface (Fig. 24). It measures 0.1 to 0.3 mm. in length and 0.031 to 0.067 mm. in width. The muscular layer is between 10 and 20 $\mu$  thick, being much more developed than those of the cirrus sac. The ductus



ejaculatorius is short, 17 to 23  $\mu$  long; the tube itself is but 3 to 4  $\mu$  in width while the muscular lining is 10 to 15  $\mu$  in depth. The small round cirrus sac occupying but one third to one half of the medullary parenchyma, ranges between 0.1 and 0.16 mm. in maximum diameter. The circular muscular layer is thin varying between 10 and 15  $\mu$  in width. The cirrus itself has a maximum length of 0.2 mm. and a diameter of 20 to 40  $\mu$ . It is filled to its distal extremity with retractile muscle fibers (Fig. 43). The circular muscles of the cirrus sac are attached ventrally to the body wall and force the cirrus out by contraction. The male reproductive system opens via a shallow male genital atrium on the ventral surface 20 to 55  $\mu$  anterior to the female system (Fig. 24).

The female genital atrium extends dorsally and posteriorly at an angle of 30 to 45 degrees. About 0.08 to 0.13 mm. from the mouth of the tube the uterus empties dorsally and laterally; the vagina continues posteriorly through a very narrow muscular neck. This soon expands giving rise to an immense receptaculum seminis measuring 0.13 to 0.27 mm. by 0.031 to 0.067 mm. This structure arises anterior to the ovarian commissure and continues up and over it, the thin walled receptaculum seminis passing well to the left of the center of the parasite in the median plane of the body. The vitelline duct passes over the ovarian commissure and crosses between it and the receptaculum seminis (Figs. 24, 43). Posteriorly this vacuity narrows and forms a small straight duct which empties directly into the oviduct. This latter part of the vagina is surrounded by a few circular muscle fibers. The anterior vitellaria (as in the case of *G. hexacotyle*) are confined to two lateral rows. This is contrary to the situation found in most of the Caryophyllaeinae, being quite characteristic of the Wenyoninae. Several of the other Caryophyllaeinae have approached this condition. The post-ovarian vitellaria are located in the usual fashion behind the wings of the ovary. The vitelline ducts descend from the anterior vitellaria and pass either just inside (i.e. median) or dorsal to the wings of the ovary. As the ovarian commissure is reached they turn medianly and unite to the left of the center. Usually a few micra from the point where the two anterior ducts empty the post-ovarian vitelline duct joins, having closely followed the left ovarian wing (Fig. 43). The common vitelline duct is short, passing medianly where it unites with the fertilization chamber (vaginal-oviducal-canal) to form the proximal end of the uterus.

The ovary differs from many of the other members of this subfamily in that it is granular in appearance instead of globular. Usually one finds the wings divided into a number of smaller divisions and while these in turn may seem granular the ensemble appears as a number of globules. These are specific differences. The wings of the ovary vary in length from 0.4 to 0.75 mm. in length and 0.1 to 0.12 mm. in width, the connecting com-

missure being relatively narrow and having an average diameter from 0.030 to 0.12 mm. In sagittal sections the commissure appears round. The oviduct arises to the left of the center by a poorly developed oöcapt which is weakly supplied with muscles. The oviduct is straight and short being 30 to 40  $\mu$  in length and 3 to 4  $\mu$  in width. The vagina joins it in the outer limits of the oötype which is smaller than was noted in other species (Fig. 43). It loops over itself, picks up the common vitelline duct and proceeds by a tortuous route to the posterior limits of the oötype where it expands into the upper end of the uterus proper. The typical uterine glands do not appear about the coils of the uterus until the duct passes the ovarian commissure enroute to the exterior (Fig. 43). The longitudinal extent of the uterus varies between one fifth and one third of the length of the testicular field; it averages just over one fourth, 26.8 percent, in measurements of 25 specimens. Fifty eggs of this species were measured and were found to average 42 by 25  $\mu$ . The actual range was from 37 to 48  $\mu$  in length and 20 to 31  $\mu$  in breadth. They appear ovoid, fairly thick shelled and contain an ovum and five or six globules of vitelline material.

*Glaridacris confusus* is placed in the Caryophyllaeinae on the basis of the appearance of the sexual apertures in the last fourth of the body length and the presence of the uterine glands and vitellaria within the inner longitudinal musculature. Since it does not possess uterine coils extending anterior to the cirrus sac it falls into one of three genera, Caryophyllaeus, Monobothrium or Glaridacris. It belongs to the latter on the basis of the type of scolex, length of the uterine coils in respect to the testicular field, the type of genital atrium and the presence of an external seminal vesicle. *G. confusus* differs from *G. catostomi*, and *G. hexacotyle* in the type of scolex, length, number of testes, size and shape of receptaculum seminis, number of excretory canals, the host and a number of minor points. It resembles *G. laruei* in the type of scolex, and differs from it in the number of testes and excretory canals, the arrangement of the vitellaria, the size and shape of the receptaculum seminis, the type of vagina and the host. A number of other differences appear upon a closer reading of the description of the forms, but these which are listed are sufficient to establish this form as a new species. It was named *G. confusus* because of its superficial resemblance to the Lytocestinae.

#### GENUS CARYOPHYLLAEIDES NYBELIN 1922

Generic diagnosis: Caryophyllaeinae with blunt, scarcely broadened anterior extremities, without a trace of specialization. Cirrus opens into utero-vaginal canal before it empties into the surficial atrium. Ovary with long wings, joined posteriorly behind the oötype, forming an inverted capital "A." Uterine coils anterior to cirrus sac, reaching a maximum longitudinal length of one-half to one-third that of testicular field. Terminal

excretory bladder and post-ovarian vitellaria present. No external seminal vesicle. Parasitic in the intestines of Cyprinidae. Development unknown.

Type species: *Caryophyllaeides fennica* (Schneider 1902).

To include: *Caryophyllaeides fennica* (Schneider 1902); *C. skrjabini* (Popoff 1924).

The validity of this genus was soon demonstrated by the description of "*Caryophyllaeus*" *skrjabini* by Popoff in 1924. He was apparently unaware of the excellent piece of work done by Nybelin (1922). But it was readily seen that by an elimination of some of the subgeneric characters from Nybelin's diagnosis that this parasite described by Popoff really belonged in this genus. His figures show two of the most diagnostic characters for the genus, the presence of the uterine coils anterior to the cirrus sac and the characteristic "A" shaped ovary. Motomura (1927) says that he omitted "*Caryophyllaeus*" *skrjabini* and "*Caryophyllaeus*" *fennica* because he was unable to find any specific differences between the two. Several differences of importance are evident from a superficial examination of the work of Nybelin (1922) and Popoff (1924). First of all the scolices are different, for *Caryophyllaeides fennica* possesses an unspecialized scolex while *C. skrjabini* has a few very weak longitudinal loculi (?). The latter possesses four rows of "Fäserzellenstränge" while Nybelin does not note any for the former. The testes number in *C. fennica* is about 150 while Popoff gives 83 as the maximum for his species. Furthermore judging from the descriptions and the figures the receptaculum seminis differs in the two; in *C. fennica* it runs in an antero-posterior direction while in *C. skrjabini* it runs dorso-ventrally at an angle of about 45 degrees with the vertical. These are a few of the differences which clearly indicate the validity of the species under consideration.

#### GENUS BIACETABULUM HUNTER 1927

Generic diagnosis: Caryophyllaeinae with well defined scolex, varying but little in shape, bearing one pair of well defined acetabular-like suckers, with or without additional loculi. Cirrus opens into the utero-vaginal canal before it reaches the surficial atrium (like *Caryophyllaeides*). Ovary "H" shaped and entirely medullary. The uterine coils extend anteriorly to the cirrus sac, reaching a maximum longitudinal extent of one fourth that of the testicular field, usually less. Terminal excretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in the Catostomidae. Development unknown.

Type species: *Biacetabulum infrequens*, Hunter 1927.

To include: *Biacetabulum infrequens*, Hunter 1927; *B. meridianum*, Hunter 1929; *B. giganteum*, Hunter 1929.



This genus has a wide distribution both as to the host and the locality. The type species was found in two specimens of *Moxostoma anisurum* (Rafinesque) which were secured through the kindness of Dr. David H. Thompson. The author had previously examined other members of the genus and found them uninfected. For example, 17 specimens of *Moxostoma breviceps* (Cope) from the same stream and general locality did not yield a single Cestodarian. During the summer of 1928 the author examined other members of the genus; these were all taken from Lake Erie. In all 6 *Moxostoma duquesnii* and 1 each of *M. aureolum*, *M. leseuri* and *M. anisurum*. None of these harbored Cestodaria. The second species was found by Dr. Fred J. Holl in *Erimyzon sucetta* from the Eno River, North Carolina. The last species was collected from both *Ictiobus bubalus* and *I. cyprinella* from various parts of the Mississippi River basin, Lake Pepin (Minnesota), the Rock River (Illinois), the Mississippi River (Iowa), and the Tallahatchie River (Mississippi). The genus was so named because of the presence of two acetabular suckers.

BIACETABULUM INFREQUENS HUNTER 1927

[Figs. 12, 16, 17, 32, 48, 69, 70, 85]

1927: *Biacetabulum infrequens*

Hunter 1927: 22

Specific diagnosis: With the characters of the genus. Adults from 16 to 22 mm. in length by about 0.6 mm. in breadth. The scolex is armed with one pair of acetabular suckers 0.168 to 0.24 mm. in diameter. Neck is distinct, having a maximum length of 0.5 mm. Body oval in cross section and posteriorly appears serrated. Cuticula 4 to 5  $\mu$  thick, followed by a subcuticula layer which is 7  $\mu$  deep and the cortical parenchyma 60 to 70  $\mu$  thick. Inner and outer longitudinal muscles are present and fairly prominent in the neck. Testes irregularly oval with maximum diameter of 0.079 to 0.168 mm. and number between 420 and 440. Cirrus sac round, occupies one-third to one-half of the medullary parenchyma, with a maximum diameter of 0.144 mm. and muscles 19 to 24  $\mu$  thick. Cirrus opens into utero-vaginal canal about 0.05 to 0.8 mm. from the ventral surface. Vagina convoluted, forms a distinct receptaculum seminis 0.105 by 0.048 mm. Wings of the ovary 0.608 to 0.658 mm. long; ovary practically fills the medullary parenchyma for the ovarian commissure is broad. Vitellaria surround the testes and measure 0.084 to 0.168 mm. in length. Excretory system has 8, 10, and 12 pairs of canals which empty into an excretory bladder 0.090 mm. long by 0.024 to 0.036 mm. in width.

Host: intestine of *Moxostoma anisurum*, Rock River, Illinois.

Type: Slide No. 29.42 in the collection of Dr. Henry B. Ward

Paratypes: Slides and vials Nos. 577.2–577.8 in the author's collection.

Host	Locality	Collector	Authority
<i>Moxostoma anisurum</i> (Rafinesque)	Rock River, Rock Falls, Illinois	D. H. Thompson	Hunter (the present paper)

During the past six years fourteen fish from the Rock River of the genus *Moxostoma* were examined. Twelve were *Moxostoma breviceps* and two were *M. anisurum*. Those from the former yielded no Cestodaria while both specimens of the latter were infected with Caryophyllaeinae. About 21 parasites were collected in all from two fish. A superficial examination showed that they belonged to the same species, for the movement, arrangement of the reproductive organs and the type and action of the scolices were identical. These parasites constituted a new genus and new species, *Biacetabulum infrequens*, Hunter (1927).

*Biacetabulum infrequens* reached a maximum length of 30 mm. while alive; the same specimens when fixed were only 20 mm. in length. Inasmuch as no eggs were found in the uteri it is possible that these individuals were sexually immature. If such is the case live adult worms would doubtless reach a length of 40 to 50 mm. However, it seems probable they were sexually mature for the testes were fully developed, much more so than is characteristic of immature forms. Furthermore, the uteri showed the presence of globules here and there which indicate that eggs had been present. It is known that parasites of fish, particularly Cestodaria, are much less plentiful in the winter than in the summer. Therefore, since these fish were examined during the first part of December the absence of eggs may be interpreted as the most conclusive bit of evidence to support the view that the parasites were adults which had already produced their quota of eggs.

The scolex is broadened laterally and tapers to the anterior extremity so that in cross section it appears nearly rectangular. The tip in one specimen was 0.2 by 0.1 mm.; this broadens rapidly until the suckers are reached. At this point the scolex is at its maximum width. It measures 0.4 mm. broad and 0.5 mm. long. In this case the greatest length occurs in an anterior-posterior direction, tapering posteriorly into the neck (Fig. 12). The suckers are two in number, these are supplemented by four small loculi which occur on the dorsal and ventral sides only. The two suckers, opposite one another in the median plane, are the most efficacious. These are flanked by the shallow loculi which are much less conspicuous and sometimes only show in sections. The latter measure between 0.24 and



0.4 mm. in depth and 0.06 to 0.12 mm. in width. The acetabular suckers are much larger in all respects. There is considerable range as is shown by the following maximum and the minimum measurements. The depth varies between 0.07 and 0.14 mm. while the width is between 0.16 and 0.24 mm. The acetabular depressions show a marked increase of the subcuticular layer which in this region is largely composed of the longitudinal muscles of the cuticula (Fig. 16).

In sagittal section the scolex may be studied to better advantage. The tip is wider and slightly rolled so that in section it appears knob-like. This knob has a diameter of about 0.15 mm. in a normally contracted specimen. It tapers posteriorly for 0.5 mm. which at the more lateral portions gives way to a pair of small depressions. Below and median to these two pairs of small loculi are found the main adhesive organs. This pair of suckers is typically acetabular. As these are paired and therefore back to back one is reminded by them of two parentheses so placed (Figs. 16, 17). They are liberally supplied with muscles from the inner longitudinal mass most of which are concentrated in large bands at the distal portions of the sucker. The concave surface of the sucker is furnished with numerous small muscles which leave the basement membrane perpendicularly and run back into the thick mass of parenchymal cells. These cells pack the scolex solidly from the posterior edge to the apex. This mass of parenchymatous tissue is interesting in several respects. In the first place muscle fibers extend from the most anterior portion of the sucker distally until they become embedded in the tip of the scolex. Other fibers leaving the basement membrane in the middle of the sucker connect with the basement membrane of the other side opposite. This arrangement undoubtedly helps to preserve the acetabular shape and at the same time aids in keeping the scolex turgid. These muscles come from the longitudinal cuticular layer which in this region has become highly specialized. At the base of this muscle layer are a series of cavities which can be traced to the main canals of the excretory system. At the posterior edge of the large acetabular suckers the parenchyma thins out into loose connective tissue for about  $60\mu$ . This connective tissue is penetrated rather freely with canals of the excretory system. On each side of the scolex an excretory tube runs anteriorly with the inner longitudinal muscles. Furthermore, muscle fibers of two sorts are found at the posterior tip of the main suckers. First there are circular muscle fibers which extend medianly about and behind the suckers; the fibers from both suckers meet in the median line. A few seem to turn posteriorly and become a part of the inner longitudinal muscle mass. This marks the limits of the parenchyma in the scolex. Other fibers having their insertion at the same spot run posteriorly to parallel the surface of the parasite. These become the outer longitudinal muscles which function in the contraction of the scolex. Behind the mass of loose connective tis-

sue occupying the cortical and medullary layers of the parenchyma for a length of 0.14 to 0.16 mm. are parenchymatous cells and most of the inner longitudinal muscles (Fig. 16). The lateral portions of the inner longitudinal muscles extend forward to the anterior tip of the scolex (Fig. 17). In the lateral parts of the scolex are numerous irregularly shaped cells whose function is not understood by the author. They are similar to those noted by Cooper (1920) and by the writer in *M. ingens*, etc.

The mechanism by which this type of scolex functions is interesting. It is evident that most of the contraction of the scolex is handled by the massive muscles of the inner longitudinal system. Expansion of the scolex, however, is a different story. Fluids in the canals of the excretory system if passed anteriorly reach the plexus of canals at the base of the scolex in the loose connective tissue. This causes an elongation of the entire scolex. Such a phenomenon would be aided by the three tubules extending to the distal portion of the scolex and also by the cross fibers which would keep the scolex from swelling laterally thereby forcing it to elongate. Essex (1928) has described a somewhat similar situation in *Corallobothrium*.

Behind the suckers the scolex begins to narrow until finally the neck is reached. This is characterized in being more oval than the testicular region; there is no sharp differentiation between the subcuticula, medullary and cortical parenchyma as is normally found. A typical specimen is really circular in cross section and measures about 0.4 mm. in diameter. As the region of the first vitellaria is reached the shape becomes more oval until it measures 0.4 mm. deep by 0.5 mm. in width. The first vitellaria appear nearly 1.3 mm. from the anterior tip in a normal adult, making the neck a rather small region averaging 0.5 mm. in length. The excretory canals are confined to the cortical parenchyma, which has now become clearly separated by the longitudinal muscles. The study of the cuticula of this species reveals that it is in essential agreement with that found in other species of the Caryophyllaeinae except that this layer is remarkably thin and measures only between 4 and 5  $\mu$  including the basement membrane. The latter, however, is less than 1  $\mu$  in thickness and is very difficult to distinguish from the cuticula proper. Beneath the basement membrane lies the narrow layer of circular muscles which become thinner posteriorly. Median to the circular cuticular layer are found the fibers of the longitudinal system. This system reaches its maximum development in the scolex where the longitudinal cuticular muscles aid in the functioning of the acetabular suckers. Four or 5  $\mu$  beneath the most median layer of cuticular muscles lie the outer longitudinal parenchymal muscles; these muscles nearly disappear posteriorly. However, they extend anteriorly and are attached to the base of the terminal disc outside the acetabular suckers. It is usual for the outer longitudinal muscles to lie

at the base of the subcuticula and to divide it from the cortical parenchyma. In this case, as in *Hypocaryophyllaeus parataris*, there appears to be little differentiation between the two. A shallow subcuticula is marked by increased pigmentation and is followed by a deeper staining cortical layer of the parenchyma. This cortical layer is characteristic and contains the canals of the excretory system. The entire distance from the edge of the cuticula to the base of the subcuticula is only about  $12\mu$ . When 4 to 5 micra are subtracted for the thickness of the cuticula (and when one realizes that beneath the cuticula are found two small sets of muscles), it is apparent that the subcuticula layer is little more than  $7\mu$  in depth. The cortical parenchyma is filled with loose connective tissue and numerous parenchymal cells. This layer if measured in the middle of the body, extends medianly for 60 to  $70\mu$  before the inner longitudinal muscles are encountered; anteriorly it is not so thick. As already mentioned this region is filled with the paired tubules of the excretory system. The musculature of the inner longitudinal mass lies about the vitellaria which in turn surround the greater portion of the testes. These muscles, lying in a nearly continuous ring about the reproductive organs, are grouped with 6 to 14 muscle fibers in a fasciculus. Anteriorly the entire neck region and the part just posterior to it are filled with the inner longitudinal muscles.

The cuticular muscles are found at the inner edge of the basement membrane, the muscles lying immediately beneath this membrane being the circular muscles. This layer extends for nearly  $1\mu$  in depth before it gives way to the longitudinal muscles of the same system. These are grouped with one or two fibers together and are situated at irregular intervals about 0.5 to  $1\mu$  apart at the inner edge of the circular muscle band. The distance from these cuticular longitudinal muscles to the outer longitudinal muscles of the parenchyma is a matter of 5 to  $7\mu$ . In the scolex the cuticular muscles become specialized as has already been described in the preceding paragraphs. Several sets of muscles comprise the group of parenchymal muscles, the inner longitudinal muscle mass being by far the most conspicuous. It is more median than any of the other muscle systems and extends posteriorly from the scolex. It forms a ring about the vitellaria and testes and this continues with little break except for the region of the cirrus sac where the continuity is lost ventrally. A few fibers leave the inner longitudinal mass and become associated with the circular fibers surrounding the cirrus sac. The muscular ring lies 0.60 to 0.13 mm. from the surface of the parasite in the neck region. However, as it passes posteriorly the inner longitudinal muscles come to lie closer to the surface. In the anterior third they are from 0.06 to 0.096 mm. from the surface, and in the region of the vas deferens it is only 0.024 to 0.072 mm. In the portion of the parasite in which the female



reproductive system lies the musculature is found to again become more median, and the muscles are from 0.048 to 0.12 mm. from the surface. In every case the distance laterally from the inner longitudinal muscles varied but slightly over the entire length of the parasite. On the other hand the dorso-ventral aspects varied between 0.028 and 0.132 mm. Doubtless even greater differences would be noted in the cases of specimens whose uteri were filled with embryos, for the distended uterus would force the muscles towards the surface. The outer longitudinal muscle mass shows more distinctly in the posterior neck region than at any other place. This layer is indistinct and lies much closer to the basement membrane than has been noted in other species of this group. The individual muscles are grouped together 3 to 5 in a fasciculus. These occur only in the region of the neck; they disappear shortly after the vitellaria commence. Anteriorly they extend well into the scolex and become inserted, as already described, on the posterior portion of the acetabular suckers. This reminds one of the condition found in *H. paratarius* and *G. laruei*. Both dorso-ventral and lateral muscle fibers show insertions in the region of the basement membrane. These are more generally spoken of as frontal (horizontal or lateral) and sagittal (dorso-ventral) fibers. The dorso-ventral muscles are slightly more numerous than those of the lateral system. These fibers appear singly and are not connected with those of the inner longitudinal system as in the case of *Capingens singularis*. Certain organs of the parasite possess highly specialized muscles, but these will be considered in the paragraphs dealing with the organ and will not be discussed in this section.

The excretory system of this parasite has certain unique peculiarities. In the first place there is no definite number of main excretory canals, for 8, 10 or 12 may be counted according to the region examined. Anteriorly the number is reduced from 10 pairs to only 8, the former being the number found in the middle of the body, while near the posterior extremity, just before passing into the excretory bladder 12 are found. In the scolex the lateral canals extend along the base of the acetabular-like sucker. These probably aid in carrying off the wastes from this field of activity, and also in the extension of the scolex. At the base of the scolex several of the canals intercommunicate and form a plexus which may aid in the extension of this organ. The fluids pass into the plexus and then out into the canals in the scolex, thus giving it turgidity and also an opportunity to carry off wastes and carry food to the cells of this locality.

The canals of this system are paired and are composed of the typical ascending and descending canals. The former lie medianly as in *M. ingens* and are usually smaller. They begin in the region of the female reproductive system, run forward and finally in the scolex or neck pass over through small canaliculi into the channels of the descending system. The

descending canals empty into the terminal excretory bladder which is approximately 0.09 mm. in length and 0.024 to 0.036 mm. in width. This bladder lies in the horizontal plane to the left of the median line from which it abruptly turns and empties to the exterior near the ventral posterior tip of the body. The terminal excretory tube is  $24\mu$  long and empties into an atrium  $48\mu$  in diameter; the atrium lies to the left of the mid line. The tube itself is lined with cuticula and the cavity is  $19\mu$  in diameter. It passes to the surface to the left of the center of the body.

The nervous system is very indistinct; two main trunks and two ganglia are visible in the neck region (Fig. 12).

The male reproductive system is composed of organs typical of the Caryophyllaeinae. The testes in this species are much more numerous than in any other species of Cestodaria studied. There are between 420 and 440 testes in the adult. This great number found in forms which reach a maximum length of 16 to 18 mm. is explained by the relatively small size of the testes and the corollary that 5 to 6 of these may be seen in transections. The arrangement of these glands is rather similar to that noted in other species, especially *M. ingens*. There are dorsal and ventral rows of testes which each contain 3 to 4 testes. The more typical arrangement, however, is an alternation which makes for compactness. Occasionally several of the testes of this species are found connected with each other, reminding one of the possibility of a common origin for several testes. This condition, however, is unusual. An examination of 50 testes from several specimens furnish the following data:

length.....	0.084-0.168 mm.
width.....	0.049-0.120 mm.
depth.....	0.069-0.096 mm.

In making measurements the length was the distance in an anterior-posterior direction and the width was the measurement laterally, while the depth was the distance in the dorso-ventral plane (Fig. 70). The vas deferens is found in the middle portion of the medullary parenchyma. It assumes a somewhat zig-zag course posteriorly, tapping the various testes and groups of testes until the region just anterior to the seminal vesicle is reached. Here the testes and vitellaria disappear from the center of the field and the vas deferens fills the entire area except for the extreme lateral portions of the medullary parenchyma which is still filled with testicular and vitellarian follicles. The vas deferens increases rapidly in size, and becomes distended with spermatozoa. The diameter, for example, of the non-distended portions is from 0.036 to 0.052 mm.; this now increases from 0.108 to 0.156 mm. in greatest diameter. In this species the expanded part of the vas deferens is more sac like than tubular, for these large cavities are free and interconnecting. Some of these long loose



convolutions extend posteriorly for 0.18 to 0.2 mm. before they recurve. As the vas deferens begins to increase in size it passes dorsally and after several convolutions crowds out the ventral testes and vitellaria and gradually assumes a rough triangular shape with the base of the triangle on the cirrus sac.

The uterus in this form, like *H. paratarius*, extends anteriorly beyond the cirrus sac. Thus the coils of the uterus begin to crowd the vas deferens ventrally and this process continues until the vas deferens is forced to the right side where it supplants the testes and vitellaria. The latter still persist near the left margin. The convolutions of the vas deferens appear earlier than the eggs in the uterus. In *H. paratarius* only a few eggs were found and yet a similar distended vas deferens was characteristic. In this species a similar situation prevails, except that no eggs appear in the uterus. The vas deferens reaches a position which is midway between the dorsal and ventral surfaces and to the right of the middle of the body. Here it forms a characteristic muscular ductus ejaculatorius which has a diameter of  $16\mu$  the walls being 4 to  $5.3\mu$  thick and the cavity 6 to  $7\mu$ . This tube passes into the seminal vesicle which lies in the ventral half of the parasite, anterior to the cirrus sac. The tube enters the right dorsal surface of the seminal vesicle. This structure slopes slightly ventrally and the long axis is towards the center of the parasite (Figs. 32, 48). This vesicle differs from all of the others which have heretofore come under my observation in that the circular muscles surrounding the cavity of the vesicle are in turn enveloped by a layer of cells. This cellular layer is 10 to  $18\mu$  thick and is composed of cells in which the cytoplasm takes little or no eosin. The nucleus stains deeply with hematoxylin and the nucleoplasm is deeply pigmented. Two deep blue nucleoli appear in the more central portion of the nucleus. From the nucleus radial thread-like structures extend across the cytoplasm to the cell wall (Fig. 69). This cellular layer shows to best advantage in a sagittal section where the cells stand out with great clearness. Under this lie the circular muscles from  $5.3$  to  $6.3\mu$  thick, while the lining of the cavity is slightly less than  $1\mu$ . The cavity has a minimum length of  $70\mu$  and a maximum length of  $135\mu$ ; the extended condition is more typical. The cavity is usually round and has a diameter of 48 to  $50\mu$ , although it may become as narrow as  $24$  by  $48\mu$ . Such variations are due to differences in contraction not only of the specimen but also of the vesicle.

The remainder of the ductus ejaculatorius is short; it leaves the seminal vesicle at its posterior end and passes dorsally past the side of the cirrus sac to a position above and more median than the seminal vesicle. The tube is from  $24$  to  $30\mu$  in total diameter and enters the cirrus sac on the anterior dorsal surface (Fig. 18). The duct is surrounded by a thin layer of circular muscles. The cells peculiar to the seminal vesicle are also present in small numbers about the muscle layer of the ductus ejaculatorius.

The cirrus sac is nearly round and has a maximum diameter of 0.144 mm. The sac is not highly muscular for the layer of circular muscles surrounding the sac are only 19 to 24  $\mu$  in thickness. The measurements of the cirrus sac in both cross and sagittal sections give a maximum width of 0.18 mm. and a length (anterior-posteriorly) of 0.225 mm. (Fig. 48). If the cirrus is extruded the cirrus sac assumes a more pyriform shape. In such cases the retractile fibers may be clearly seen extending from the apex of the cirrus and the base of it to the walls of the cirrus sac opposite the point of exit of the cirrus. Measurements of the extruded cirrus in three specimens gave the following data:

length of cirrus extruded.....	0.168–0.192 mm.
diameter of cirrus at apex.....	0.055–0.065
diameter of cirrus in middle.....	0.067–0.072
diameter of cirrus at base.....	0.069–0.074
diameter of urethra.....	0.019–0.024

The musculature of the cirrus showed to good advantage in the sagittal sections. In one specimen the cirrus was not fully extruded, but the arrangement of the muscles showed clearly. The contraction of the circular muscles forced the cirrus out. This was indicated by the contracted appearance of the muscles and by the fact that in an unextruded specimen the tube which pierces the cirrus is loosely coiled within the confines of the sac. Longitudinal muscle fibers extend from the distal tip of the cirrus to the median walls of the cirrus sac. Other fibers run from the base of the cirrus to the median wall of the sac. The cirrus sac is flanked laterally by the arms of the ovary which extend anteriorly beyond it. The cirrus sac and the female cloaca open into a common atrium, which is 48 to 50  $\mu$  in depth and serves as a cloaca for both the male and the female reproductive systems. The male system, however, empties from the anterior side into the utero-vaginal canal coming ventrally from a position directly dorsal (Fig. 48). In this respect the male system resembles that of the genus *Caryophyllaeides*, Nybelin (1922).

The ovary is lobate and assumes the "H" shape so characteristic of the *Caryophyllaeinae*. The commissure which connects the two main arms of the ovary is nearly circular and has a diameter of about 0.168 mm. The length of the main arms varies from 0.6 to 0.65 mm. Anteriorly they extend beyond the cirrus sac, even in relatively uncontracted specimens. The ovary fills the bulk of the medullary parenchyma and is 0.182 to 0.253 mm. in depth. The ovarian commissure lies slightly ventral to the mid line and divides the ovary into two equal parts. The commissure also serves as an ovarian reservoir. The oöcapt takes its origin from the median ventral side. It consists of a circular sphincter muscle 7 to 9  $\mu$  in thickness which guards the entrance into the oviduct and controls the release of the ova. The vagina appears in the same section above the ovarian commissure. It leaves

the female cloaca on the posterior side a little ventral to the point where the uterus empties in from above. Immediately the vagina becomes distended into a large receptaculum seminis. This measures about 0.1 mm. in length and has a maximum width of 0.048 mm. (Fig. 32). The receptaculum seminis is filled with spermatozoa. These are typically flagellate and measure 10 to 11  $\mu$  in length. The head piece is 2.1 by 0.8 to 1  $\mu$ . The vagina passes posteriorly and dorsally until it reaches a position directly above the ovarian commissure. It is at this point that the oöcapt leaves the commissure ventrally (Fig. 85). The vagina then passes ventrally, to the left and goes into the oötype along with the vitelline duct and the oviduct. The vagina is surrounded throughout most of its course by a layer of circular muscles 5 to 7  $\mu$  thick which in turn is covered with a layer of cells. The oviduct arising from the distal end of the oöcapt passes ventrally and then to the left where it is immediately joined by the vagina which has passed down from a position dorsal to the ovarian commissure. The union of these two ducts marks the formation of the fertilization chamber, or the vaginal-oviducal canal. This duct passes posteriorly for a short distance before it is joined by the unpaired vitelline duct, coming from the anterior part of the body. This passes ventrally and turns up to meet the vaginal-oviducal canal from the posterior ventral side. Thus the uterus is formed; it passes through the highly glandular oötype to the posterior regions of the body. The uterus, after leaving the oötype is thin walled, and the characteristic uterine glands only make their appearance when the most posterior part of the uterus is reached. These glands persist and are found around the convoluted uterus until it has passed the cirrus sac and reached its most anterior position and started posteriorly to empty into the female cloaca. The uterine glands are present until the last two convolutions of the uterus are reached where they gradually disappear. The vitelline ducts are paired in the anterior body parts. These canals are situated laterally to the vas deferens which runs up the center of the worm. Posterior to the region of the cirrus sac the two canals fuse and become one. The post-ovarian vitellaria lie distally to the uterus. A single duct arising medianly runs anteriorly and joins the main vitelline duct before it empties into the vaginal-oviducal canal. The eggs of this species are not present in the available material. Even though the female reproductive system is apparently fully developed no eggs are found in the distal positions of the uterus. As this material was not secured until the winter it is possible that they were taken at a season when the parasites were sexually inactive. However, it is also possible that this parasite normally would not become sexually mature until the following spring.

*Biacetabulum infrequens* because of its monozootic nature, coupled with the arrangement of the reproductive organs, clearly falls into the Caryophyllaeidae. The form belongs in the Caryophyllaeinae owing to the



medullary position of the inner longitudinal muscles which surround the vitellaria. It is excluded from the genera *Caryophyllaeus*, *Monobothrium* and *Glaridacris* by the shape of the scolex and the uterine coils which never extend anteriorly to the cirrus sac. *Biacetabulum infrequens* is also excluded from the genus *Archigetes* on the basis of the scolex, excretory system, host and the possession of a caudal vesicle bearing the embryonic hooks. The only other possibilities which remain lie in the genera *Caryophyllaeides* and *Hypocaryophyllaeus*. The former is barred by the specialization of the scolex, shape of the ovary, and the maximum distance the uterine coils extend in relation to the testes. It differs from the latter in the type of scolex, the longitudinal extent of the uterine coils in relation to the cirrus sac as well as the type of genital atrium. It was therefore necessary to create a new genus and species to hold this form, *Biacetabulum infrequens* Hunter (1927).

*BIACETABULUM MERIDIANUM* HUNTER 1929

[Figs. 15, 34, 46, 47, 64, 65, 90]

1929: *Biacetabulum meridianum*

Hunter 1929: 190

Specific diagnosis: With the characters of the genus. Adult parasites 5 to 15 by 0.4 to 0.8 mm. Scolex fairly prominent and is set off from the body which is flattened dorso-ventrally by a well defined neck. Cuticula 4 to 6  $\mu$  thick; underlaid by thin subcuticula 6 to 16  $\mu$  deep followed by cortical parenchyma 50 to 70  $\mu$  thick. Cuticular, outer and inner longitudinal muscles, all present and prominent. Testes 65 to 95 roughly oval, with maximum diameter from 0.13 to 0.15 mm. Vas deferens confined medially between uterine coils; short ductus ejaculatorius precedes "L" shaped seminal vesicle 0.13 to 0.27 mm. long, extending from the ventral to the dorsal surface of the medullary parenchyma. Cirrus sac round, occupies one-fourth to one-half of the medullary parenchyma; diameter from 0.13 to 0.2 mm.; circular muscles of this organ 10 to 15  $\mu$  thick. Male reproductive system opens into the combined utero-vaginal canal 0.04 to 0.07 mm. from the outside. Vagina median, convoluted and forms crescent shaped receptaculum seminis about 70  $\mu$  in length just before passing over ovarian commissure. Ovarian wings are 0.3 to 0.4 mm. by 0.9 to 0.15 mm. The last third of the uterus not surrounded by typical uterine glands and this portion lies anterior to ovarian commissure. Vitellaria with maximum diameter of 0.08 to 0.13 mm. Eight pairs of main excretory canals terminating in excretory vesicle 45 to 60  $\mu$  long by 20 to 25  $\mu$  wide. Eggs oviform 48 to 54 by 31 to 37  $\mu$ .

Host: *Erimyzon sucetta*, Eno River, North Carolina. In intestine.

Type: Slide in the collection of Dr. Henry B. Ward, No. 29.43

Paratypes: Slides and bottled material in author's collection, No. 687.2-687.6.

Host	Locality	Collector	Authority
<i>Erimyzon sucetta</i> (Lacépède)	Eno River, Durham, N. C.	F. J. Holl	Hunter (the present paper)

The material forming the basis for the description of this species was collected by Dr. F. J. Holl while at Duke University, Durham, N. C. He examined 14 specimens of *Erimyzon sucetta* and only found three or 21.4% infected. These three according to Dr. Holl's records harbored 1, 50 and 73 Cestodaria respectively. The author examined several specimens from the vicinity of Urbana, Illinois, during 1925 and 1926 but did not find any infected with Cestodaria.

These parasites present the typically monotonous external form which is characteristic of the Caryophyllaeinae. The scolex appears slightly broader than the remainder of the body (Fig. 15). It measures 0.4 to 0.6 mm. in longitudinal extent and 0.4 to 0.55 mm. in width. The widest part is the base of the scolex, just posterior to the two main suckers which lie on the median dorsal and ventral surface. These acetabular-like suckers are 0.15 to 0.25 mm. in diameter in cross section and 0.2 to 0.27 mm. in a longitudinal plane, are rather shallow and measure 70 to 100  $\mu$  in thickness. This is the distance from the bottom of the cup to the back of the cup and is sometimes designated as base to back. The suckers are only weakly acetabular in nature and do not stand out as distinctly as those of *B. infrequens*. The outer longitudinal muscles are attached to the proximal margin of the sucker while most of the inner longitudinal fibers are dissipated on the distal margins of the cup (Figs. 64, 65). Some of these are not attached to the sucker but pass directly to the distal portion of the scolex. The acetabular nature of the scolex is brought out in figure 65 which also indicates a certain motility of the suckers. Evidently it is possible for them to create a lot of suction and no doubt are capable of some motion and rotation due to the nature of the musculature. Throughout the scolex are found a number of muscle fibers; these extend dorso-ventrally and also laterally.

Within the medullary parenchyma are found two ascending tubes of the excretory system. Before the suckers are reached these tubes pass laterally and connect with a ring which extends around the cortical parenchyma of this organ and gives off several pairs of descending canals. In the neck these tubes divide giving rise to 8 which number remains constant throughout the body. The two ascending tubes from the medullary parenchyma have now become subdivided and paired with their mates of the descending system. These pass posteriorly through the cortical parenchyma while the descend-



ing tubes empty posteriorly into the small terminal excretory vesicle. Like others this vesicle is pear-shaped and at its proximal end (which is also the widest part of the bladder) the descending canals empty; it is only 45 to 60  $\mu$  in length and 20 to 25  $\mu$  broad and is lined throughout by a continuation of the cuticula.

The neck is somewhat narrower than the body and varies from 0.3 to 0.6 mm. in length and 0.2 to 0.4 mm. in width. The musculature is clearly discernible here, even the small cuticular muscles. In this region the cortical parenchyma reaches a maximum width of 95 $\mu$  and the medullary parenchyma is correspondingly reduced; no change in the thickness of the subcuticula was noted. In the body proper this layer remains very thin being only 6 to 15  $\mu$  deep. Towards the outside and embedded in this are the longitudinal and circular cuticular muscles, while the outermost limits of the subcuticula are bounded by a poorly defined basement membrane. This layer constitutes the innermost one of the cuticula which is only 4 to 6  $\mu$  thick. At the inner edge of the subcuticula lies the outer longitudinal muscles which separate this from the adjoining layer of the cortical parenchyma. These muscles contain but two or three fibers per fasciculus and these in turn are located 5 to 15  $\mu$  apart. The distance of this layer from the outside changes but little. At the innermost margin of the cortical parenchyma lie the more prominent inner longitudinal muscles containing 6 to 10 individual fibers in each fasciculus. This layer lies between 60 and 90  $\mu$  of the outside of the parasite except in the neck and base of the scolex where the fibers are drawn closer to the center of the body and the distances reach a maximum of about 120  $\mu$  (Figs. 65, 90).

The testes number from 65 to 95, are generally ovoid in shape and possess a maximum diameter of 0.13 to 0.16 mm. In cross section there is a dorsal and ventral row bounded laterally by vitellaria. There occur two to three testes per row and as many vitellaria. As the cirrus sac is approached the testes and vitellaria in the mid regions are displaced by the invading uterine coils. Just anterior to and between these occur the thin walled twisted vas deferens. This may occupy but a small part of the medullary parenchyma even when filled with spermatozoa, as only the mid dorsal portion of the medullary parenchyma is occupied. Laterally it is surrounded by the uterine coils and the vitellaria, altho in specimens which contained empty vas deferentia the major part of this organ lay anterior to the invading uterine coils and not median to them. The coils of the vas deferens have a maximum diameter of 30 to 47  $\mu$ . The ductus ejaculatorius arises from the most median ventral coil of the vas deferens; it passes ventrally only 30 to 50  $\mu$  before expanding into the more muscular seminal vesicle. This vesicle is prominent and "L" shaped, much longer than wide, extending posteriorly and dorsally at an angle of about 30 degrees with the vertical. It turns on itself and dips towards the ventral surface, passing into another short

narrow portion of the ductus ejaculatorius before penetrating the cirrus sac (Fig. 46). The seminal vesicle is 0.13 to 0.27 mm. in length and 0.03 to 0.05 mm. in width; the layer of circular muscles varies from 6 to 9  $\mu$  in thickness. The cirrus sac is round and has a maximum diameter of 0.139 to 0.2 mm.; the circular muscles are thin being 10 to 15  $\mu$  thick. The cirrus sac is tilted at a slight angle so that the cirrus opens posteriorly into the utero-vaginal canal of the female reproductive system which in turn is even with the surface.

This canal, as the name implies, is composed of two elements, the uterus and the vagina. It extends in a dorso-ventral direction. The male reproductive system empties 0.04 to 0.07 mm. from the ventral surface. The vagina proceeds posteriorly and ventrally while the uterus comes in from an anterior dorsal position. Just prior to its union with the vagina to form the utero-vaginal canal there is a well defined sphincter muscle which regulates the discharge of the eggs (Fig. 46). The vagina continues on its ventral swing until close to the inner longitudinal muscles where it becomes somewhat straighter and continues posteriorly in a convoluted path until the ovarian commissure is reached. The receptaculum seminis is formed anterior to the ovarian commissure but level with middle of the ovarian commissure; it runs dorsally and is completed as the vagina passes over the commissure. (See Figs. 46, 47.) The cavity is 0.06 to 0.08 mm. long and 0.015 to 0.025 mm. in width. It is somewhat crescent shaped and is surrounded by a layer of circular muscles 4  $\mu$  deep. After passing the ovarian commissure the vagina dips to the left and posteriorly until nearly the end of the ovarian wing where it curls on itself and winds medianly to the spot where it joins the oviduct to form the fertilization chamber (Fig. 34). The vitellaria are present as two lateral rows joined by an intersprinkling of these glands between the testes which they tend to surround. They are joined anteriorly to the testes and the lateral vitellaria extend posteriorly to within 50  $\mu$  of the ovary (Fig. 34). Post-ovarian vitellaria are also present. The vitelline glands range in size from 0.08 to 0.13 mm. in maximum diameter which normally is found in a dorso-ventral plane. The ducts arise in the mid line just median to the two lateral rows of testes, they continue posteriorly until the ovary is reached. As usual these canals pass median to the ovarian wings and over the ovarian commissure. In doing this the vitelline ducts are lateral but on the same plane as the vagina and the uterus. Posterior to the commissure the left vitelline duct is joined by one from the post-ovarian vitellaria which followed the inner longitudinal muscles closely (Fig. 47). These united ducts pass laterally as a vitelline reservoir and are joined by the one from the right side, thus forming the common vitelline reservoir, and later duct.

The globular ovary is "H" shaped with ovarian wings varying from 0.3 to 0.4 mm. in length and 0.13 to 0.16 mm. in width. The commissure of this

gland is posterior to the center and measures 0.09 to 0.12 mm. in cross section. The oviduct arises from the ventral posterior portion of the commissure by means of a well defined oöcapt which is  $20\ \mu$  in diameter. The muscles are 5 to  $6\ \mu$  thick and the whole structure is funnel shaped with most of the muscles at the base of the flare of the funnel. The oviduct is only about  $50\ \mu$  in length; it passes posteriorly to the left in an arc which carries it anteriorly again. It is at the outer edge of the oötype and is joined by the vagina, forming the fertilization chamber; this canal continues posteriorly describing a larger reverse arc for over  $100\ \mu$ , picking up the common vitelline reservoir duct about the middle of the body and but  $50\ \mu$  from the beginning of the fertilization chamber. Immediately after uniting with the vitelline duct a number of glands of the oötype are passed (Fig. 47). The uterus continues by numerous convolutions posteriorly through the oötype finally passing dorsally to form the ascending limb of the uterus proper which is surrounded by the typical uterine glands. After passing the ovarian commissure the uterus becomes highly convoluted which continues until the cirrus sac is passed. This area is filled dorsally, ventrally and laterally except for a single row of vitellaria along the side. As the uterus bends posteriorly again, the uterine glands begin to disappear, so that most of one loop from the cirrus sac to the ovarian commissure and back (until anterior to the cirrus sac again) is composed of a uterine tube devoid of the typical uterine glands. Instead is a layer of circular muscles which are 2 to  $3\ \mu$  in thickness. Approximately one third of the uterus is so lined. Just before the uterus joins the vagina there is the uterine sphincter which has previously been described (Figs. 34, 46). The eggs are oviform and measure  $48$  to  $54\ \mu$  by  $31$  to  $37\ \mu$ .

This parasite clearly belongs in the genus *Biacetabulum* on the basis of the scolex, acetabular sucker and type of genital atrium. *Biacetabulum meridianum* differs from the type species, *B. infrequens*, in the development of the one pair of acetabular suckers, which are more highly specialized in the case of the type species. It is natural that the arrangement of the reproductive systems should have much in common; the testes, however, number 65 to 95 in *B. meridianum* compared with 420 to 440 in *B. infrequens*. Likewise the vitellaria are typically smaller in the type species altho the maximum diameters are essentially the same (Fig. 90). The seminal vesicle is much larger and longer in *B. meridianum* than in *B. infrequens* measuring 0.13 to 0.27 mm. compared with a maximum of 0.107 mm. for the latter species. Furthermore the layer of deep staining cells so characteristic of the type species is absent from *B. meridianum* and the receptaculum seminis is consistently smaller in the latter species and is located closer to the ovarian commissure. The excretory vesicle is smaller and the 6 pairs of excretory canals remain unchanged in *B. meridianum*. Other important differences which should be stressed are (1) the thickness of the cirrus sac muscles,



which is greater in *B. meridianum*, (2) the position of the vas deferens here confined to the region between the coils of the uterus while in the type species it is found at one side, (3) the uterine coils, which are without the characteristic uterine glands, are confined to regions anterior to the cirrus sac in *B. infrequens* while in *B. meridianum* they extend to the ovarian commissure and back in addition, (4) the well defined sphincter muscle of *B. meridianum* and (5) the hosts of the two parasites are different. This brief summary constitutes the main points of difference between these forms. This new species herein described was named *Biacetabulum meridianum* to denote the locality from whence it came.

*BIACETABULUM GIGANTEUM* HUNTER 1929

[Figs. 18, 33, 40, 53-60]

1929: *Biacetabulum giganteum*

Hunter 1929: 190-191

Specific diagnosis: With the characters of the genus. Adults 7 to 16 mm. by 0.8 to 1.08 mm.; posterior half of body flattened dorso-ventrally. Scolex resembling the well developed "II" type, bearing four loculi, and two median well developed acetabular-like suckers. Cuticula 7 to 9  $\mu$  thick; subcuticula and cortical parenchyma reduced to a minimum in the posterior half of the body, together are 0.038 to 0.070 mm. thick. Medullary parenchyma occupies three fourths to seven eighths of body width. Inner longitudinal musculature reduced to eight fasciculi in the base of the scolex; outer longitudinal muscles prominent throughout the body as are the cuticular muscles. Testes irregularly oval, 0.12 to 0.2 mm. in greatest diameter and number 165 to 215. Vas deferens may fill entire medullary parenchyma; seminal vesicle 0.13 to 0.2 mm. by 0.08 to 0.12 mm. Ductus ejaculatorius straight, about 0.15 mm. long. Cirrus sac ovoid, 0.22 to 0.27 mm. in diameter; the muscles are 33 to 47  $\mu$  thick. Cirrus opens into utero-vaginal canal. Vagina ventral, straight, thick-walled and forms a receptaculum seminis 0.060 to 0.142 mm. by 0.035 to 0.06 mm. Ovarian wings 0.37 to 0.54 mm. by 0.16 to 0.23 mm. Vitellaria surround the testes and are 0.13 to 0.23 mm. in maximum diameter. Excretory system has 8 pairs of canals; the descending canals empty into an excretory vesicle 40 to 60  $\mu$  long by 18 to 25  $\mu$  in width.

Host: *Ictiobus bubalus* and *Ictiobus* sp., Tallahatchie River, Mississippi. In intestine.

Type: Slides of author's material in the collection of Dr. Henry B. Ward, No. 29.44.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota. Slides and vials Nos. 628, 651.2, also 653, 655, and 659 in author's collection.

Host	Locality	Collector	Authority
<i>Ictiobus</i> sp.	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
<i>Ictiobus bubalus</i> (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
<i>Ictiobus bubalus</i> (Rafinesque)	Mississippi River Fairport, Ia.	—	Hunter (the present paper)
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

This species was found in the Mississippi collection of Dr. Parke H. Simer. The parasites were of moderate size, 7 to 16 mm. in length by 0.8 to 1.08 mm. in breadth, while the body was divisible into a well defined scolex, neck and body. The scolex resembled the *Glaridacris* "II" type and is 0.67 to 1.0 mm. long by 0.67 to 1.3 mm. wide. Of the six organs of adhesion which were visible the median acetabular ones appeared to be the most efficacious. These were oval and resembled suckers in totos; they measured 0.4 to 0.5 mm. long and 0.27 to 0.3 mm. wide (Fig. 18). At the base of the scolex the diameter becomes highly reduced as it passes into the narrow neck. The scolex is filled with bundles of muscles, some inserted on its flat distal portion. One tenth mm. from the tip the number of fibers is increased and the mid region is dotted with a mass of individual fibers. (These are represented slightly out of proportion in Figs. 54-60.) As the loculi are reached the scolex becomes cut by these and in each projecting ridge of tissue between them is a bundle of muscles traceable to the inner longitudinal system. Through this region are also found numerous transverse and dorso-ventral cuticular muscles (Figs. 56-58). The two median depressions resemble true suckers more closely than the other four, and these are not only deeper, but much larger. As in *B. infrequens* the cuticular muscles connect the base of the suckers back to back; nuclei are also found concentrated in this area (Figs. 56-58). As the lower end of the scolex is approached the muscles are drawn together and concentrated into eight fasciculi, four in each lateral third of the scolex as in *G. confusus* (Figs.



57-60). The base of the scolex (Fig. 60) shows the fasciculi more equally scattered and as the neck is reached these become more concentrated until practically the entire medullary parenchyma is filled. Canals of the excretory system are present from the region of the loculi posteriorly and are very prominent in the neck.

The neck is rather long and narrow being 1.2 to 2.6 mm. in length and having a maximum width of 0.3 to 0.47 mm. The middle region is filled with muscles which posteriorly become pushed aside, the space becoming filled with the reproductive organs. The cuticula is well defined and 7 to 9  $\mu$  thick. This layer takes the stain quite evenly throughout. Beneath it lie the cuticular muscles, the circular and longitudinal muscles having a combined thickness of 4 to 5  $\mu$ . These are situated in the subcuticular layer of the parenchyma which varies between 8 and 20  $\mu$  in depth; it is usually about 10  $\mu$  except in the neck where it becomes thicker. At the inner edge of this layer is a well defined set of outer longitudinal muscles which are 5 to 7  $\mu$  thick and consist of three to five muscle fibers per fasciculus. The cortical parenchyma is bounded medianly by the inner longitudinal muscles; it is 30 to 50  $\mu$  thick and in the neck is sometimes 75  $\mu$  deep. The inner longitudinal musculature is by far the most conspicuous muscle layer and is normally 10 to 15  $\mu$  in thickness, but reaches a maximum of 60  $\mu$  in the neck. In this region it fills the entire parenchymal field.

The excretory system is remarkably clear in this form and will consequently be described at some length. The canals are paired, there being 8 pairs of main canals in all of the specimens examined. The inner one is slightly smaller and has a thicker wall. At the beginning of the neck the 8 pairs of inner canals fuse to form 4 and each pair invades the medullary parenchyma of the neck. These in turn are reduced to 2 pairs as the base of the scolex is approached. They preserve their integrity until the anterior part of the scolex is reached where the internal pair fuses with its companionate descending tubule. The shape of this scolex must remain relatively unchanged since there are so few excretory canals in this region. These outer tubules pass back through the scolex (as previously noted) divide in the neck, pass to the cortical parenchyma and proceed posteriorly to the excretory bladder. This vesicle 40 to 60  $\mu$  long and 18 to 25  $\mu$  wide, in cross section is serrate; the reduced cuticula extends inwards as the lining of this cavity. There are of course a number of smaller intercommunicating canals, but it is impossible to trace these out in preserved material.

The testes numbering 165 to 215 are irregularly spherical to ovoid in shape and measure 0.16 to 0.2 mm. in maximum diameter. In the last third of the testicular field the vas deferens becomes noticeable. This assumes a central position while the two vitelline ducts are located more laterally; they lie just median to the lateral rows of the vitellaria (Fig. 53). In cross section there are usually two to three testes in the dorsal and ventral rows although

this number may be augmented occasionally. As the posterior limits of the testicular field are passed the vas deferens expands and frequently fills the entire medullary parenchyma at least in a dorso-ventral plane; the maximum diameter varies between 0.1 and 0.21 mm. (Fig. 33). However this does not occur in specimens in which the vas deferens is not swollen with spermatozoa. It gradually narrows down to pass into the seminal vesicle which is 0.13 to 0.2 mm. in length. In spite of its central appearance in figure 33 it is more normally found to the left of the cirrus sac. The main axis of the seminal vesicle is in a dorso-ventral plane and is surrounded by a layer of circular muscles 15 to 26  $\mu$  wide while the cavity is 0.1 to 0.2 mm. long by 0.06 to 0.1 mm. wide; it is penetrated from the dorsal surface and passes ventrally into a short straight ductus ejaculatorius which is about 0.16 mm. long and penetrates the cirrus sac from the median anterior surface. The muscles which line the vessel are 7 to 9  $\mu$  thick and the tube itself is 15  $\mu$  wide making a total diameter of about 30  $\mu$ . The cirrus sac is fairly small having a diameter of 0.2 to 0.27 mm. and a heavy layer of muscles which varies between 33 and 47  $\mu$ . The general shape is round and there are nuclei found occasionally scattered through the muscles as well as within and without the layer. The extended cirrus is 0.13 to 0.2 mm. in length and about 0.033 mm. in breadth. The cirrus sac opens into the utero-vaginal canal (Fig. 40).

The utero-vaginal canal extends dorsally for about 0.1 mm. before it gives off the vagina which leaves and remains close to the median ventral surface of the medullary parenchyma. It is relatively straight, and is only 7 to 8  $\mu$  wide and thin walled. As it approaches the ovarian commissure it crosses to the right and passes over the middle of the commissure and in so doing forms a receptaculum seminis. This structure is lined by a cuticula-like substance, followed by 2 to 4  $\mu$  of circular muscles which in turn are bounded by a cellular layer 5 to 15  $\mu$  in thickness. The receptaculum seminis varies from 0.06 to 0.125 mm. in length and 0.035 to 0.05 mm. in width; it passes over the vitelline ducts and dips ventrally into the oötype complex where it joins the oviduct 60 to 80  $\mu$  from its point of origin. The vitellaria surround the testes and are from 0.13 to 0.23 mm. in maximum diameter. The vitelline ducts descend in the usual manner, meet just dorsal to the ovarian commissure, and pick up a duct from the right margin of the post-ovarian vitellaria (cf. *G. confusus*). The ovary is 0.37 to 0.54 mm. by 0.16 to 0.23 mm. It is globular in contrast with *G. confusus* and is quite small compared with many species, even in well expanded specimens (Fig. 33). The ovarian wings are so broad that the commissure is quite short and has a maximum diameter of 0.14 mm. The oviduct arises from the middle of the ovarian commissure about mid way between the dorsal and ventral surfaces. It arises through a small oöcapt, passes posteriorly for 20 to 30  $\mu$ , turns up for 40 to 50  $\mu$  and unites with the vagina at the peak of the arc.

The two form the fertilization chamber. This continues posteriorly through the oötype for about  $25\ \mu$  before uniting with the common vitelline duct. After a number of convolutions in the oötype the uterus emerges close to the anterior edge of the post-ovarian vitellaria, becomes surrounded by the typical uterine glands, dips dorsally and then proceeds anteriorly keeping to the right of the center as in *H. paratarius*. These uterine coils extend anteriorly to the right side of the cirrus sac and then drop back to position a dorsal to the cirrus sac where it crosses to the left side, and extends anteriorly to the vas deferens before winding posteriorly to its point of exit. It crosses under the vagina to the right side, comes back to the median line and dips ventrally where it picks up the vagina one half the way down to the outside. No eggs were found in the uterus. The forms examined showed all signs of sexual maturity except the presence of eggs. In fact small particles of vitelline material were found in sections of the uterus which pointed to the probable extrusion of the ova at sometime in the not very distant past.

*Biacetabulum giganteum* is placed in this genus on the basis of the type of scolex; the uterine coils, which extend anteriorly to the cirrus sac and the manner in which the male reproductive system opens into the utero-vaginal canal. It resembles the type species in the general way the reproductive system is formed, but differs in several important features; the type and shape of the scolex which bears six distinct indentations in this new species; the greater thickness of the cuticula; the size and number of the testes, the size, shape and musculature of the cirrus sac; the shortness of the ovarian wings in *B. giganteum*, the comparative narrowness of the ovarian commissure; the excretory system which has a definite number of tubules (8), and the excretory bladder which is larger in the type species; and finally the hosts themselves.

*Biacetabulum giganteum* differs from *B. meridianum* in the following respects: the scolex is larger and resembles the "II" type; the cuticula is thicker, being 7 to  $9\ \mu$  compared with 4 to  $6\ \mu$ ; the testes number 165-215 to 65-95 for *B. meridianum*; the cirrus sac and its muscles measure respectively 0.22 to 0.27 mm. and 33 to  $47\ \mu$  compared with 0.13 to 0.2 mm. and 10 to  $13\ \mu$  and finally both the size of the vitellaria and the host differ greatly. *Biacetabulum giganteum* was so named because of the proportionately large size of its scolex and other organs.

#### GENUS HYPOCARYOPHYLLAEUS HUNTER 1927

Generic diagnosis: Caryophyllaeinae with three pairs of loculi on a poorly defined scolex. Cirrus opens on ventral surface or into a shallow non-eversible genital atrium. Ovary "H" shaped and entirely medullary. Uterine coils extend anteriorly to cirrus sac, reaching a maximum longitudinal extent of one-fourth or less that of the testicular field. Terminal ex-



cretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in the intestine of Catostomidae. Development unknown.

Type species: *Hypocaryophyllaeus paratarius*. Hunter 1927.

To include: *Hypocaryophyllaeus paratarius* Hunter 1927.

The members of this genus are confined exclusively to fish of two genera of the Catostomidae, *Carpiodes* and *Ictiobus*. Both genera are fairly closely alike in feeding habits and in natural habitat. When these fish were seined we often secured both genera in the same haul. This was done time and again along the Mississippi River. The type species was found only in fish from the Rock River in Illinois and the Mississippi River near Fairport, Iowa. The genus was named *Hypocaryophyllaeus* because of the small size of the type species.

#### HYPOCARYOPHYLLAEUS PARATARIUS HUNTER 1927

[Figs. 5-7, 27, 37, 38]

1927: *Hypocaryophyllaeus paratarius*

Hunter 1927: 22-23

Specific diagnosis: With the characters of the genus. Adults 7 to 10 mm. by 0.15 to 0.3 mm., flattened dorso-ventrally. Scolex bears 6 weak loculi and is roughly wedge shaped. Cuticula is 3 to 6  $\mu$  thick, and the subcuticula and cortical parenchyma have a combined width of 30 to 73  $\mu$ . The latter figure is more typical of the adults. Medullary parenchyma occupies about one-half of the body width. Inner longitudinal muscles reduced to 8 fasciculi in the neck. Outer longitudinal muscles only found in the neck and soon disappear. Testes number 60 to 85 and are very small measuring 80 to 100  $\mu$  by 43 to 55  $\mu$ . Cirrus sac occupies two-thirds of the medullary parenchyma with maximum diameter of 0.105 mm., the circular muscles of 12 to 15  $\mu$ . Male and female reproductive systems open on the surface 50  $\mu$  apart. Vagina straight and forms a distinct receptaculum seminis 0.125 to 0.135 mm. in length, very thick walled, being surrounded with circular muscles of the same thickness as those found about the cirrus sac proper. Vitellaria surround the testes with maximum diameter of 52 to 73  $\mu$ . Six pairs of main excretory canals. Eggs of this species small, ovoid, non-operculate, 26 to 32 by 18 to 21  $\mu$ .

Host: *Carpiodes carpio*, *Carpiodes velifer* and *Ictiobus cyprinella*, from the Rock and Mississippi rivers, Illinois and Iowa. In intestine.

Type: Slides No. 29.45 a-b in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota. Slides and vials No. 274, 304.2-304.3 in the collection of the author.

Host	Locality	Collector	Authority
<i>Carpiodes carpio</i> (Rafinesque)	Rock River, Sterling, Illinois Mississippi River, Ia.	J. F. Müller G. W. Hunter, III	Hunter (the present paper)
<i>Carpiodes velifer</i> (Rafinesque)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)

The material furnishing the basis for the description of this species was secured from members of the family Catostomidae, the genera *Carpiodes* and *Ictiobus*. The bulk of the parasites were found in the upper half of the intestinal tract of *Carpiodes carpio*. Most of the fish came from the Rock River, although some of the material came from the Mississippi River.

*Hypocaryophyllaeus paratarius* is characterized by a rather long thin body which tapers posteriorly to a distinct apex. The length of the adult specimens varies from 7 to 10 mm. in length and 0.15 to 0.3 mm. in breadth. The average width based upon the measurements of 14 adults is 0.215 mm. The scolex is a poorly defined structure, capable of considerable variation in shape and size due to the extreme development of the longitudinal muscles which extend to its anterior extremity; in life there is considerable variation in the size and shape of the scolex due to the contraction of the aforementioned muscles. In preserved material, as in life, the scolex is wider than the remainder of the body and measures 0.25 to 0.28 mm. in length and 0.3 to 0.56 in width and bears upon the dorsal and ventral surface three pairs of ill-defined loculi (Fig. 5). Of these six loculi the central one is the most efficacious. Even in the contracted specimens the suckers are shallow and are not provided with hooks of any sort.

*Hypocaryophyllaeus paratarius* is further characterized by an unusually large amount of subcuticular and cortical tissue. This species is unique, for this layer constitutes nearly one-half the width of the parasite. It confines the reproductive organs to unusually narrow limits. One specimen, for example, gave the following data, the cuticula and subcuticula measured 0.055 mm. while the total width of the parasite was only 0.22 mm. This case clearly shows that the vitellaria and testes are confined to a region nearly one half the width of the worm. Such a condition is characteristic for the species. The testes lie in two irregular rows and are surrounded



laterally by the vitellaria, which in turn are surrounded by the inner longitudinal muscles. By actual count there are between 60 and 85 testes in the sexually mature adults. The testes of several parasites ranged from 88 to 100  $\mu$  in length and 52 to 55  $\mu$  in width. The vitellaria of the adults show variation in size; measurements give a length of 52 to 73  $\mu$  and a width of 24 to 38  $\mu$ . Post-ovarian vitellaria are present. The female reproductive system is confined to the posterior fifth of the body. This character is specific for *H. paratarius*.

The scolex is broader than the body and has an indefinite shape (Fig. 5). In cross section the six loculi appear, although they are universally weak (Fig. 27). Differences in degree of contraction do not alter the shape in cross section which tapers anteriorly to a rather blunt wedge shaped tip (Fig. 6). The inner longitudinal muscle band is heavy many of the fibers extending to the lateral portions of the scolex where they become lost in the region of the loculi; some simply go into the wall of the scolex and are embedded in the basement membrane (Fig. 6).

The cuticula of this species is moderately thin, varying between 3 and 6  $\mu$ ; it is somewhat thinner in the scolex. In young specimens the cuticula is thicker than in the adults and measures 4 to 5  $\mu$ . The average width of the cuticula based upon data from 12 specimens, young and adults, was 4.3  $\mu$ . The cuticula is composed of an outer layer which does not stain readily and an inner basement membrane which is about one-third of the total width. As in some of the other closely related forms the cuticula and cortical parenchyma cannot be readily separated. The medullary parenchyma is marked off by the type of cells and the presence of the inner longitudinal muscles. Since it is nearly impossible to separate the subcuticula and the cortical parenchyma it will be considered as a single layer. This varies from 30 to 77  $\mu$  in thickness. The narrowest width occurred in a young specimen measuring less than 1.5 mm. in length and the maximum was found in the adults. If only the adults were considered the limits of variation are 61 to 77  $\mu$ . Beneath the basement membrane of the cuticula lie the circular cuticular muscles followed by those of the longitudinal system. At intervals of 20 to 30  $\mu$  are found small ducts perforating the cuticula. These come from large glandular like cells lying just median to the longitudinal muscles and probably either function in the secretion of the cuticula-forming substance or are concerned with nourishment. The former hypothesis seems more reasonable since these cells are not connected with the organs within the medullary parenchyma. Between the longitudinal cuticular muscles and the inner longitudinal muscles are found the canals of the excretory system. Both the ascending and descending ducts penetrate this tissue. Also numerous dorso-ventral and lateral muscle fibers are present. The inner longitudinal muscles, by far the most prominent muscle system in the body, surround the vitellaria which in turn are arranged an-

nularly about the testes. This runs from the anterior tip of the scolex to the posterior portion of the body. The continuity of these muscle bundles is threatened posteriorly as the last fifth of the body is reached and is finally broken when the muscle bands along the ventral side give way to the cirrus sac of the male reproductive system. The longitudinal musculature forms a ring in the posterior portion of the body within which lie the reproductive organs. This muscle system lies at the inner edge of the cortical parenchyma and separates it from the medullary parenchyma. As the neck region is approached the individual muscle bundles are gradually drawn together into eight large fasciculi, so that the muscles pass to the scolex in four lateral (two at each end), two dorsal and two ventral bundles. The bundles are soon broken up and their contents dissipated to the apex of the scolex while a few strands disappear into the inner surface of the loculi and the basement membrane of other portions of the scolex (Fig. 27). There are dorso-ventral muscles but these appear to have their origin in isolated cells and are found scattered throughout the parenchyma of the body. A few lateral muscle fibers are also found. Two other muscle layers should be noted, a small layer of longitudinal muscles and outside of that a circular muscle layer with a thickness of 0.9 to 1.0  $\mu$ , lying beneath the basement membrane. These form the musculature of the cuticula and are known as the cuticular system. The most highly specialized musculature is found in the cirrus sac and the muscular seminal vesicle. The latter is in reality a muscular sac which possesses the ability of rapid and spasmodic contraction thereby acting as a pump and forcing the spermatozoa which are stored in the vas deferens, out through the cirrus. The muscles which surround the cirrus sac are of the same type as those about the seminal vesicle. Upon the contraction of these circular muscles the cirrus is extruded. Thus there are two sets of highly specialized circular muscles, the ones about the seminal vesicle forcing the spermatozoa out through the ductus ejaculatorius and the cirrus which has already been extended through the action of the cirrus sac musculature. A third specialized muscle is the small sphincter of the oöcapt less than 1  $\mu$  in diameter, which regulates the discharge of ova from the ovarian commissure.

The excretory system is composed of 6 pairs of main longitudinal canals which run the length of the body. In the adult specimens the walls of the system measure 1.5  $\mu$  to 1.7  $\mu$  and the total diameter is between 11 and 12  $\mu$ . These are connected by numerous passages the diameters of which are slightly less than those of the main canals. From these cross ducts extend minute canaliculi each of which eventually subdivides until a small excretory cell is reached. Anteriorly in the scolex the excretory canals break down into innumerable smaller canals, and these penetrate the base of the scolex. Posteriorly the 6 descending canals join to form a single short

excretory duct which terminates in a poorly defined excretory vesicle. This varies between 37 to 45  $\mu$ ; the pore has a diameter of 2  $\mu$ .

The nervous system shows indistinctly, even in the material which was stained with iron hematoxylin. The system is composed of two main nerve trunks. These extend posteriorly from the base of the scolex where the two ganglia are joined by commissures. The nerve strands give off several large branches to the inner longitudinal muscles. The nerves can be traced posteriorly only as far as the beginning of the testes. Shortly thereafter the strands seem to break up into plexuses as in the case of *Glavidacris catostomi* Cooper (1920).

The testes lie in a double row within the inner longitudinal muscle bands. The counts show that the testes number between 60 and 85, the usual count being about 74 to 76. These are surrounded by the vitellaria and the latter by the longitudinal muscle bands. The testes do not extend as far anteriorly as do the vitellaria. Measurements of the young specimens (1.5 to 2.5 mm. in length) show that the testes do not begin until the middle of the body. In adults 25 of the oval testes measures from 80  $\mu$  to 100  $\mu$  in length and 43 to 55  $\mu$  in width (Fig. 38). These seem to be contiguous medianly with the curves and twistings of the vas deferens. In other words, the vasa efferentia are so reduced in length, if they are present at all, as to be negligible. The vas deferens curves in a zig-zag fashion from one testicle to the other, the median posterior border of the testes being connected with the walls of the vas deferens. This vessel runs near the median line between the testes, and leaving them passes into the parenchymatous region which lies between these organs and the cirrus sac. This region is primarily occupied by the convolutions of the thin walled vas deferens, but in it are also found several loops of the uterus. The vas deferens leaves the testicular field medianly and immediately the walls become swollen. A close examination shows this canal to be filled with minute spermatozoa. This duct passes dorsally and posteriorly making three convolutions, then passes ventrally and approaches the longitudinal muscle layer. The coils of the thin walled vas deferens pass posteriorly and ventrally to the muscular seminal vesicle. The wall of the vas deferens varies from 1 to 1.5  $\mu$  while the diameter of the spermatozoan-filled posterior portion of the vas deferens is from 19 to 43  $\mu$ . As the vas deferens passes under the seminal vesicle the thin walled surface gives way to a much thicker, narrower tube. This tube, the ductus ejaculatorius, has a diameter of 11.5  $\mu$  and the walls are 3  $\mu$  thick, which means a tubular width of only 5.5  $\mu$ . It passes dorsally and enters the muscular seminal vesicle anteriorly at its ventral surface (Fig. 38). In sagittal section the seminal vesicle measures 98 by 84  $\mu$  and is surrounded by a layer of circular muscles. Within the muscular coat lies a cavity or reservoir 50 by 28  $\mu$  in length, lined with tissue having a thickness of 3  $\mu$ . At the posterior end of the cavity



lies the remainder of the ductus ejaculatorius extending ventrally into the cirrus sac. This is  $48\ \mu$  in length and 7 to  $8\ \mu$  in width. The lining of the duct is  $2\ \mu$  thick and is of the same character as that which lines the seminal vesicle. The cirrus sac is a prominent organ found near the ventral surface of the parasite in the posterior region of the body. The sac is  $105\ \mu$  in diameter and is surrounded by circular muscles which, when contracted, extend the muscular cirrus. The circular muscles which comprise the outer layer of the cirrus sac vary between 12 and  $15\ \mu$  in thickness. The muscle mass is thickest on the ventral surface (Fig. 38). Here the muscles are essential to retain the shape of the groove through which the cirrus is extruded when the remainder of the circular muscles contract. The cirrus is  $12\ \mu$  in diameter. The lining of this organ appears as a continuation of the cuticula and is  $3.1\ \mu$  in thickness. The cirrus sac opens into a very shallow atrium of its own approximately  $50\ \mu$  anterior to the female genital atrium.

The ovaries are situated laterally and in the rough assume the characteristic "H" shape. Those of the younger specimens resemble a bunch of grapes, and are globular. Later in adult life the contour of the individual units of the ovary is lost and only the general "H" shape remains (Fig. 37). The cross arms of the "H" forms the ovarian commissure. The ovaries from 0.1 to 0.2 mm. in length and 0.067 to 0.1 mm. in width. The oöcapt arises from this and runs ventrally. It is less than  $10\ \mu$  long, is composed of weak circular muscles and gives rise to the oviduct into which empties the vagina through a small opening which is guarded by a small sphincter muscle. The opening within the limits of the muscle has a diameter of less than  $1\ \mu$  in both the oöcapt and vaginal sphincters. This cavity is large enough to permit the passage of ova when the circular muscles are not contracted (Fig. 38). The ova at this point have a diameter of about  $7\ \mu$ . The vagina broadens out and passes dorsally into the receptaculum seminis. This structure is not highly specialized and is not therefore readily distinguishable from the vagina proper. The tissue lining the vagina increases from 2 to  $3\ \mu$  in thickness which may be accounted for by the presence of an additional layer of glandular like cells. These cells contain globules which resemble vitelline material. This receptaculum seminis has a length of 125 to  $135\ \mu$ . After leaving this specialized portion of the vagina the walls again thin out to  $2\ \mu$  and the surrounding cellular layer is lost. After a series of convolutions the main descending limb of the uterus is joined from the side and the vagina and uterus empty by a common duct, the cloaca, into the shallow female genital atrium  $50\ \mu$  posterior to that of the male (Figs. 37, 38).

The vitellaria surround the testes in an irregular annular ring. They extend anteriorly beyond the testes and are present behind the ovary as a group of post-ovarian vitellaria. In size these glands measure from 52 to  $73\ \mu$  in length and 24 to  $38\ \mu$  in width. The two main vitelline ducts

lie in the lateral medullary parenchyma. They pass the ovary medianly and unite to form a single common vitelline duct, which connects with a single duct from the post-ovarian vitellaria, before disappearing into the oötype to unite with vaginal-oviducal canal to form the uterus. The uterus proper takes its origin just ventral to the spot where the vagina empties into the oviduct forming the vaginal-oviducal canal which is formed by the juncture of the common vitelline duct ventral to the vagina. After making several convolutions the uterus passes into a deep "U" shaped semicircle, surrounded by much loose glandular material. This structure is part of the oötype and shell gland. Several specimens show eggs in the process of shell formation. The whole series of ducts are at this point filled with vitelline material. The uterus remains thin walled as it leaves the shell gland and oötype and passes laterally and anteriorly. As the posterior tip of the right half of the ovary is passed the uterus becomes surrounded by numerous deep staining pear shaped glandular cells. The exact function of these cells is not known. The uterus then proceeds medianly, still remaining on the right side and runs with several smaller convolutions dorsal to the oviduct. It makes several deep twists and then passes to the left side and its coils extend anterior to the cirrus sac where it undergoes numerous convolutions; eventually reaching a position posterior and dorsal to the cirrus sac. The uterus then descends rapidly, joins the vagina and passes as already described, into the female genital atrium. The eggs are small thin shelled and ovoid, non-operculate measuring 26 to 32  $\mu$  in length by 18 to 21  $\mu$  in width.

*Hypocaryophyllaeus paratarius* undeniably belongs to the Caryophyllaeinae and this therefore raises the question of a genus to hold this species. It resembles Caryophyllaeus in nearly all respects except the uterine coils which lie anterior to the cirrus sac, the presence of an external seminal vesicle, the longitudinal extent of the uterus in relation to that of the testes and the fact that it is found only in the Catostomidae. Likewise this form cannot be classed as a member of the genus Glaridacris on account of the uterine coils and the longitudinal extent of the uterus which is one-fourth or less that of the testes. *Hypocaryophyllaeus paratarius* in no wise resembles a species of the genus Monobothrium and it corresponds to Caryophyllaeides only in respect to the position of the uterine coils. It differs in type of ovary, length of the uterine coils in relation to the longitudinal extent of the testes, type of scolex and the host. The genus Biacetabulum, upon the other hand, differs from *H. paratarius* in possessing a Caryophyllaeides-like genital atrium and in being characterized by a distinct scolex bearing acetabular-like suckers. Since *H. paratarius* fits into none of the aforementioned genera the author erected a new genus, *Hypocaryophyllaeus*, to hold this form. (See Hunter 1927.)



## GENUS ARCHIGETES LEUCKART 1878

Generic diagnosis: Caryophyllaeinae with well defined, hexagonal-shaped scolex, bearing two bothria-like depressions. Cirrus opens into the utero-vaginal canal before it reaches the surficial atrium (like Caryophyllaeides?). Ovary "H" shaped and medullary. Excretory system without terminal vesicle, but with numerous ampullae at the posterior end of body. Uterine coils extend anteriorly beyond the cirrus sac, and vas deferens expands to form an external seminal vesicle. Caudal vesicle carrying embryonic hooks. Parasitic in body cavity of Tubificidae.

Type species: *Archigeters sieboldi* Leuckart 1878.

To include: (1) *A. sieboldi* Leuckart 1878. (2) *A. brachyurus* Mrázek 1908. (3) *A. cryptobothrius* Wisniewski 1928.

## SUBFAMILY LYTOCESTINAE HUNTER 927

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated in the last quarter of the body length. The inner longitudinal muscles lie *entirely internal* to the vitellaria which are annularly arranged about the muscles in the cortical parenchyma. Uterine glands are present.

Type genus: *Lytocestus* Cohn (1908).

## GENUS LYTOCESTUS COHN 1908

Generic diagnosis: Lytocestinae in which the scolex is unspecialized and not broader than the remainder of body. Male and female genital pores open on the surface behind one another and not into a common atrium. Two rows of main longitudinal muscles, the outer one being cortical and internal not external to the nuclear layer of subcuticula. Longitudinal extent of the uterus is at the most one third that of testicular field. Ovarian follicles cortical, only ovarian commissure being medullary. Uterus does not extend anterior to wings of ovary which is "H" shaped. Post-ovarian vitellaria absent. Parasitic in Mormyridae and Siluridae.

Type species: *Lytocestus adhaerens* Cohn, 1908.

To include: (1) *L. adhaerens* Cohn, 1908. (2) *L. filiformis* (Woodland, 1923). (3) *L. indicus* (Moghe, 1925).

At the present time this genus constitutes a refuse pile into which are cast many questionable forms. Some belong here without question. Such for example is the case of *L. filiformis* (Woodland 1923). Fuhrmann and Baer (1925) placed this form in the genus *Lytocestus*, along with *L. chalmersius* (Woodland 1924). These authors state at the time that while the descriptions of both forms are inadequate they clearly belong to

the genus *Lytocestus*. However, from reading a description of *L. chalmersius* this author feels very strongly that a restudy of the parasite in question may lead to its being placed in the new genus created by Fuhrmann and Baer (1925), *Monobothroides*. In the first place, the type of scolex is the same in both forms, as each possesses a terminal introvert and a number of furrows extending longitudinally. Further than this the arrangement of the reproductive organs appears essentially similar, so that this author feels confident that it really belongs in the genus *Monobothroides*. The writer has therefore tentatively placed this form in the aforementioned genus.

Woodland (1926) suggests that Moghe's "*Caryophyllaeus*" *indicus* probably belongs in the genus *Lytocestus*. Allowing for the misinterpretation of several structures it appears quite probable that the form really does belong in that genus, altho it should be redescribed in greater detail. On the authority of Woodland (1926) the writer placed Johnston's (1924) "*Balanotaenia*" *bancrofti* in the same group (Hunter 1927). Since then access to the original paper of Johnston has established the validity of the genus (Hunter 1929). According to Woodland (1926) the "*Caryophyllaeus*" *noliticus* of Kulmatycki (1924) is *W. virilis* Woodland 1923.

#### GENUS BALANOTAENIA JOHNSTON 1924 char. emend.

Generic diagnosis: *Lytocestinae* (?) possessing little specialization of the scolex, except longitudinal loculi and a circular muscular "frill" which is folded and thick when contracted. Male reproductive system opens separately or into a common genital atrium on the ventral surface. Ovary "H" shaped and only the isthmus (ovarian commissure) is entirely medullary. Main inner longitudinal muscles lie partially *internal* to the testes as two parallel sheets frequently broken up by strands which go about and between the testes. Uterine coils do not extend anteriorly to the cirrus sac and have a maximum length less than one-half the length of the testicular field. Post-ovarian vitellaria absent. Parasitic in the intestine of Siluroids. Development unknown.

Type and at present only species: *Balanotaenia bancrofti* Johnston 1924.

As noted above *Balanotaenia bancrofti* was relegated to the genus *Lytocestus* in a previous publication (1927) on the authority of Woodland (1926). At that time this author did not know the location or publication of the original description of this parasite. Since locating the work it appears that the genus belongs in the "*Lytocestus* group" and hence falls into the subfamily *Lytocestinae*. Likewise it is apparent that there are sufficient characters to warrant the retention of this form as a valid genus.

## GENUS MONOBOTHROIDES FUHRMANN AND BAER 1925

Generic diagnosis: Lytocestinae with scolex devoid of bothria, but bearing numerous longitudinal furrows, and possessing a terminal introvert. Male and female reproductive systems open on the surface by two separate pores. Uterus never passes anteriorly to the cirrus sac and is present as a long regularly wound tube. Post-ovarian vitellaria absent. Ovary "H" shaped, coils of uterus extend anterior to wings of ovary. External seminal vesicle present. Parasitic in the intestines of the Siluridae.

Type Species: *Monobothroides cunningtoni* Fuhrmann and Baer, 1925.

To include: (1) *Monobothroides cunningtoni* Fuhrmann and Baer, 1925.  
(2) *Monobothroides chalmersius* (Woodland 1924) (?).

As noted previously *L. chalmersius* is provisionally placed in this genus by this author on the basis of the scolex with a terminal introvert and the numerous longitudinal furrows. The male and female reproductive systems open separately. Unfortunately the exact position of the uterine coils in relation to the cirrus sac could not be ascertained from Woodland's figures, but the uterus appears to be regularly coiled. There are no post-ovarian vitellaria, the ovary is "H" shaped and the uterine coils extend anteriorly to the wings of the ovary. The presence or absence of an external seminal vesicle could not be determined. There appear to be enough characters to warrant placing this species provisionally in the genus, for it is certainly more closely allied to it, than to *Lytocestus*.

## GENUS DJOMBANGIA BOVIEN 1926 Char. emend.

Generic diagnosis: Lytocestinae with globular scolex armed with terminal sucker, circular in shape bearing acetabular affinities. Male and female reproductive systems open into common genital atrium near the posterior end of body (?). Ovary "H" shaped, entirely medullary (?). Uterine coils extend anteriorly to cirrus sac nearly as far as testicular field thus forcing testes to edges of medullary parenchyma. Post-ovarian vitellaria absent. Eggs covered with spines. Parasitic in intestine of *Clarias* sp. Development unknown.

Type and at present only species: *Djombangia penetrans* Bovien 1926.

This genus clearly belongs in the subfamily Lytocestinae altho several of its diagnostic characters could not be definitely determined from the original description of Bovien (1926). Thus the figures show beyond doubt the location of the sexual apertures as well as the position of the vitellaria in relation to the inner longitudinal muscles. Furthermore the uterine glands are present in this form. In the generic diagnosis it was impossible to determine whether or not the ovary was entirely medullary for no sections were given which showed this. Judging from the location of the



vitellaria and the testes in the toto mount it was possible to deduce that the ovary would be medullary rather than cortical in position. Another point which could not be ascertained from the figures of Bovien (1926) is whether or not the male reproductive system opens into the female utero-vaginal canal or into a common atrium. The figure leads one to the conclusion that the male system opens into the female, for it more closely resembles the type of atrium described for *Caryophyllaeides* Nybelin (1922) than *Caryophyllaeus*.

#### GENUS LYTOCESTOIDES BAYLIS 1928

Generic diagnosis: Lytocestinae with short conical scolex, not broader than the rest of the body and devoid of bothria. Vitellaria superficial, forming a continuous layer which surrounds the testes and other organs and continue laterally to post-ovarian vitellaria. Testes arranged internally to the vitellaria, usually forming a layer. Male and female reproductive systems open into shallow common genital atrium in the last fourth of the body length. Uterus relatively short. Excretory canals, at least in the posterior region of the body, internal to the vitellaria. Parasitic in the digestive tract of a fish (probably *Alestes* sp.). Development unknown.

Type and at present only species: *Lytocestoides tanganyikae* Baylis 1928.

In the original description of this genus and species Baylis noted that the material was in a poor state of preservation. Hence many of the details of the musculature, etc. could not be made out. Baylis (1928) noted the proximity of the vitellaria to the body surface as well as the location of the excretory canals internal to the vitellaria. These he pointed out were reasons for supposing that the inner longitudinal muscles were probably located internally to the vitellaria, since in all other species the main longitudinal muscle system lies about, or in the medullary parenchyma and the excretory canals are external to this. Another indication that this genus belongs in the Lytocestinae lies in the regular shape of the vitellaria. This author pointed out (Hunter 1929) that the vitellaria were only irregular in shape when they were squeezed in passing between the strands of the inner longitudinal muscles to reach the cortical parenchyma. Since this condition is only found in the Capingentinae (*Pseudolytocestinae*) where these glands have a medullary origin their regular shape in the case of this genus may be taken as additional evidence of their belonging in the Lytocestinae.

#### SUBFAMILY CAPINGETINNAE NEW SUBFAMILY

SYNONYM: *Pseudolytocestinae* Hunter 1929

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated in last fifth of the body. The inner longitudinal muscles *partly*

*internal* to vitellaria which arise and extend for one third to one half their length in medullary parenchyma where they are typically annularly arranged about the muscles in cortical parenchyma. Uterine glands present.

Type genus: *Capingens* Hunter 1927.

The only difference between this subfamily and the *Lytocestinae* lies in the relation of the vitellaria to the inner longitudinal muscles. In cases where the separation is clear cut we find the muscles functioning as a complete wall or sheath. In the case of this subfamily the vitellaria originate within the inner longitudinal muscles but much of their bulk is forced between the strands of the muscles and so extrude into the cortical parenchyma for one third to one half their bulk. Since this difference is constant in the various genera and species and differs from the *Lytocestinae* proper it appeared advisable to create a new subfamily and place therein all the genera possessing vitellaria which extrude into the cortical parenchyma for one third to one half their bulk. This was done in a previous paper (Hunter 1929). Phylogenetically this subfamily no doubt lies between the *Caryophyllaeinae* and the *Lytocestinae*. Since *Capingens* was the first genus of this group to be described it was taken as the type genus (Hunter 1929). At that time the group was erroneously designated as *Pseudolytocestinae* which was of course incompatible with the assignment of *Capingens* as the type genus.

#### GENUS CAPINGENS HUNTER 1927

Generic diagnosis: *Capingentinae* possessing a definite scolex which occupies one-fifth to one-fourth total body length and bearing one pair of well defined bothria. The scolex does not vary in shape as in the other *Cestodaria*. Vitellaria extend into cortical parenchyma past inner longitudinal muscles having their origin within medullary parenchyma. These glands form a continuous row laterally with post-ovarian vitellaria. Cirrus opens on ventral surface or into a shallow genital atrium which is non-eversible and is anterior to similar atrium for female system. Uterine coils lie anteriorly to cirrus sac and reach a maximum longitudinal extent of one-third or less that of testicular field. External seminal vesicle present. Parasitic in *stomach* of *Catostomidae*. Development unknown.

Type and at present only species: *Capingens singularis* Hunter 1927.

*Capingens* is one of the most interesting genera of the *Caryophyllaeidae*. Upon first examining the scolex one is impressed with the superficial similarity to the *Bothriocephalid* tapeworms. Further study serves only to accentuate the likeness which is primarily one of musculature. Sections of the scolex of *Capingens singularis* compares very closely with that of *Bothriocephalus microcephalus* Rud. Indeed within this group lies



real morphological evidence of a relationship between the Caryophyllaeidae, the Ptychobothriidae and the Cyathocephalidae. Here the likeness ends for the remainder of the organization of the parasite is clearly that of the Caryophyllaeidae.

As noted in a previous publication (Hunter 1929) this genus was removed from the Lytocestinae where it was originally placed and taken as the type genus of the Capingentinae. At the time of the original description note was made of the medullary origin of the vitellaria, but it was not until several more forms were discovered with a similar arrangement that any systematic significance was placed upon it. After further study these were all grouped together in the subfamily, Capingentinae. The genus name was formed from "caput" and "ingens" to denote the great size of the scolex.

CAPINGENS SINGULARIS HUNTER 1927

[Figs. 10, 11, 35, 73-77]

1927: <i>Capingens singularis</i>	Hunter 1927: 24
1928: <i>Capingens singularis</i>	Baylis 1928: 561
1929: <i>Capingens singularis</i>	Hunter 1929: 186

Specific diagnosis: With the characters of the genus. Adult parasites ranging from 4 to 8 mm. in length and 1.08 to 1.5 mm. in maximum breadth (which occurs in the scolex). Neck indistinct and is in reality absent for the reproductive organs extend into the base of the scolex. Maximum body width (exclusive of the scolex) is 1.23 mm. Body oval in cross section; cuticula 3 to 4  $\mu$  in thickness. Subcuticula 5 to 6  $\mu$  deep, followed by the cortical parenchyma which is 30 to 45  $\mu$  across. Inner and outer longitudinal muscles present although the latter are not prominent. Testes are 210 and 225 in number and have a maximum diameter of 0.06 to 0.108 mm. Cirrus sac round, occupies three-fourths of the medullary parenchyma and is from 0.216 to 0.264 mm. in diameter. Circular muscles 24 to 36  $\mu$  in thickness. Male and female reproductive systems open on the surface 60 to 70  $\mu$  apart. Vagina convoluted, does not form a receptaculum seminis. Ovary globular and very short, nearly surrounding the cirrus sac, 0.25 to 0.35 mm. in length; possesses an extremely narrow ovarian commissure only 24 to 36  $\mu$  in diameter. Oviduct 80 to 90  $\mu$ . Vitellaria take their origin in the medullary parenchyma but extend past the inner longitudinal muscles and into the cortical parenchyma, and are 36 to 60  $\mu$  by 14 to 24  $\mu$ . Excretory canals numerous and average about 25 to 30 pairs of longitudinal canals in cross section. Excretory vesicle 40  $\mu$  by 19 to 24  $\mu$  and lies in a horizontal plane. Ovoid eggs 40 to 45 by 21 to 26  $\mu$ .

Host: stomach of *Carpiodes carpio*, Rock River, Illinois, and *Ictiobus urus*, Lake Pepin, Minnesota.

Type: Slide No. 29.46 in the collection of Dr. Henry B. Ward.

Paratype: Slide No. 422.1 in the collection of the author.

Host	Locality	Collector	Authority
<i>Carpiodes carpio</i> (Rafinesque)	Rock River, Rock Falls, Ill.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
<i>Ictiobus urus</i> (Agassiz)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

Two specimens of *C. singularis* were obtained in examinations covering nearly six hundred fish of the family Catostomidae. It is evident that this species is rare and occurs infrequently in the genera of fish examined. However, the habitat and external appearance of this parasite mark it as unique among the Caryophyllaeidae. It is found embedded between the folds of the mucosa and submucosa in the stomach of its host. During the summer of 1925 *C. singularis* was first encountered in the stomach of *Carpiodes carpio* taken from the Rock River at Rock Falls, Illinois. (Essex and Hunter (1926) give a general account of this expedition.) Later, while at Lake Pepin on the Mississippi River another specimen was found in the stomach of *Ictiobus urus*. Both hosts were of good size, the first measuring 25 cm. and the other 50 cm. One specimen was stained and mounted in toto, the other was sectioned.

*Capingens singularis* is very regular in shape. The scolex is large, prominent and measures about 1.13 mm. occupying one-fourth of the body length. On the dorsal and ventral surfaces of the scolex are immense bothroid suckers measuring 0.8 to 1.03 mm. in length (Fig. 10). Behind these suckers is a constriction indicative of the neck. The body gradually becomes more pointed as the posterior tip is approached, which is bluntly rounded. The length of this species varies from 4.22 to 6 or 8 mm.; the maximum width which occurs in the scolex is 1.08 to 1.53 mm. The neck measures 0.7 to 0.9 mm. while the maximum body width is 1.23 mm. The width anterior to the cirrus sac is about 0.6 mm. while posterior to it the breadth is 0.55 mm. Several other distinguishing characters can be seen in a toto mount. The vitellaria are small and lie in 10 to 15 rows paralleling the longitudinal axis. The testes are unusually small lying in 7 to 8 parallel rows. The cirrus sac is prominent and the coils of the uterus extend anteriorly to it.

The scolex of this species is very prominent and occupies about one-fourth of the body length (Fig. 10). It is roughly rectangular in shape, bearing two large and deep efficacious suckers upon its flattened dorso-ventral surface. These suckers are distinctly bothroid and are of immense

size. As has been noted in the preceding paragraphs it extends in a posterior direction and measures from 0.8 to 1.0 mm. in length and 0.5 to 0.6 mm. in width. The depth of this sucker is from 0.15 to 0.25 mm. The following table gives a summary of the measurements based on the toto mounts and the cross sections of the specimens. The musculature of

*Measurements of Suckers of C. SINGULARIS*

Length (anterior-posterior).....	0.8–1.0 mm.
Breadth (at surface).....	0.5–0.6
Breadth (at base of sucker).....	0.20–0.30
Depth of sucker.....	0.15–0.25

the scolex and the sucker is of interest. The inner longitudinal muscles are very prominent and numerous fasciculi are present, each containing as many as fifty individual muscle fibers. These bundles of muscles penetrate into the scolex, which is much wider than the body. The inner longitudinal muscles start curving towards the cuticula. Many of these become lost in the basement membrane of the posterior portion of the sucker (Fig. 11). Other fibers continue anteriorly. The cuticular muscles of the scolex surrounding the suckers become highly specialized for the circular layer has thickness of 20 to 30  $\mu$ . Likewise the longitudinal cuticular muscles are highly developed and may be seen throughout the scolex as dorso-ventral and lateral muscle fibers. The former connect the suckers back to back, while the latter run from their sides to the lateral portions of the scolex (Fig. 11). The scolex resembles a capital "I" in cross sections. The remaining fibers of the inner longitudinal system are found medianly as the suckers deepen, and those which are not inserted from time to time on the basement membrane of the suckers ultimately reach the more distal portions of the scolex. A few of the longitudinal muscle fibers become specialized as diagonal muscles. The cells of the parenchyma are scattered throughout the scolex indiscriminately. The canals of the excretory system are present in the base of the scolex and extend anteriorly for some distance as canaliculi but do not break up into as many canaliculi as in *M. ingens*. The descending branches unite to form the main descending excretory canals. No neck is present, for in both specimens the reproductive organs first appear in the base of the scolex.

The cuticula is composed of a layer 3 to 4  $\mu$  in thickness of which the lower third goes to form the basement membrane. The cuticula becomes slightly thinner in the scolex, although at this point the muscles of the scolex become highly specialized. In the median and posterior body parts the circular cuticular muscles form a layer less than 1  $\mu$  in width, beneath which are found the longitudinal muscles of the same system. Between the basement membrane and the outer longitudinal muscles lies the subcuticula. This layer is non-nucleate and is largely filled with connective tissue and lateral or dorso-ventral muscle fibers which branch



before passing between the longitudinal cuticular muscles to their insertions on the basement membrane. This subcuticular layer is only 5 to 6  $\mu$  in thickness and its limits extend from the basement membrane to the beginning of the nucleated cortical layer and the few scattered outer longitudinal muscles of the parenchyma. These occur in small groups some 30 to 45  $\mu$  outside the inner longitudinal system. This latter very prominent group marks the beginning of the medullary parenchyma. Within the cortical layer are found the main tubes and tubules of the excretory system. The greater number of the vitellaria lie externally to the inner longitudinal muscles, and external to these are the canals of the excretory system surrounded with masses of nuclei. There are also numerous round parenchymal cells; these have a heavy cell wall and the nuclei stain deeply. Numerous myoblastic cells are also present.

The arrangement of the musculature of *C. singularis* is somewhat unusual. The cuticular muscles are quite indistinct except in the scolex. They are composed of the circular and longitudinal sets of fibers; the former lying close beneath the basement membrane and the latter situated medianly to the circular layer. In the scolex both sets of fibers become highly developed, especially in the region of the acetabular suckers, where the circular muscles develop into a layer 20 to 30  $\mu$  in thickness. Likewise the bulk of the fibers which connect the backs of the suckers and those extending to the more lateral portion of the scolex arise from the longitudinal cuticular system. Five to 6  $\mu$  from the basement membrane are found the outer layer of the longitudinal parenchymal muscles. Several fibers are grouped together and lie just externally to the nucleated cortical parenchyma. These fibers are more plentiful in the anterior parts of the body and are found in greater numbers near the dorsal and ventral surfaces. Where these muscles are found in the posterior body parts they often appear as single strands; this is particularly true of the region about the cirrus sac and posterior to it. The inner longitudinal muscles are readily distinguished for they stand out with great clarity. Lying 30 to 45  $\mu$  more medianly than the outer longitudinal muscles and having as many as 50 or more individual fibers in each fasciculus they dominate the field so as to readily attract the eye. These large groups of muscles measure between 16 to 32  $\mu$  in greatest diameter (Fig. 73). The disposition anteriorly of these muscles has been described in detail in the paragraphs dealing with the scolex and will not be reconsidered here. Posteriorly the inner longitudinal fibers gradually converge so that as the excretory vesicle is reached they assume a position about this cavity, the majority of these muscles becoming embedded in its walls. However a few extend past this cavity and are attached to the basement membrane in the posterior extremity. Dorso-ventral and lateral muscles fibers are present in considerable numbers throughout the body. Both sets of fibers inter-

minge freely with those of the inner longitudinal system. The dorso-ventral fibers are present in greater numbers than those of the lateral system; they aid in keeping the body shape of the parasite and also in holding the reproductive organs in position.

The excretory system is comprised of a series of main ascending and descending canals, the former are situated closer to the surface than the latter. In general the entire system resembles that described by Fraipont (1880) for *Caryophyllaeus*. The ascending canals are smaller than those of the descending system and are formed by small canaliculi which in turn are composed of several renal corpuscles uniting to form the caniculus. These cells are not the typical flame cells but resemble the renal corpuscle described by Cooper (1920). These are large cells, and take a deeper stain than the parenchyma. They are round with radiating fibers of cytoplasm extending out to the wall of the vesicle in which they lie. These fibers take a lighter stain than the remainder of the cell body and some take an eosin counter stain. This suggests the possibility that these renal corpuscles, which lie at the expanded distal end of a canaliculus, contain muscular fibrillae which have the ability to contract and in so doing force the liquid wastes accumulated in this cavity out through the canaliculus to the ascending canal. Evidence for this view may be found in the way these cells or portions of them took the counter stain, and also by the fact that a few of these cells are found in a more contracted state than some of the others which was indicated by a thickening of the fibrillae and the walls of the ducts lying closer to the walls of the renal cell. As is the case with the flame cell the renal corpuscle caps the expanded portion of the canaliculus, only a portion of it lying in the cavity of the canal itself (Fig. 77).

Both series of canals are so irregular in their course that it was impossible to determine the number of main ascending or descending canals. In one cross section, for example, the number of times the descending canals are cut numbers over thirty. This is typical of the sections. In the scolex the ascending canals are scarcely broken up and do not permeate the scolex as is the case in some of the other species described. This fact may be interpreted as evidence for the view that the excretory system plays a part in the extrusion of the scolex, which in this species shows but little movement when living material is studied.

The descending canals extend posteriorly and lie within 10 to 20  $\mu$  of the inner longitudinal muscles passing into the excretory vesicle from the side. This vesicle lies horizontally, 70  $\mu$  from the outside, measures 40  $\mu$  in length and has a maximum diameter of 19 to 24  $\mu$ . The bulk of the inner longitudinal muscles become attached to the sides of the excretory vesicle. Apparently it is derived from the outer layers for the cuticula is continued as a lining of the vesicle. It narrows posteriorly and passes at right angles into a narrow canal leading to the ventral surface. This canal



is 42 to 50  $\mu$  long and 4 to 9  $\mu$  wide; it is slightly inclined towards the posterior tip. This canal in turn empties into a large excretory atrium which is 36 to 48  $\mu$  in diameter and 20 to 30  $\mu$  in depth. The atrium and the canal emptying into it are lined with cuticula identical with that found elsewhere on the surface of the parasite.

The testes are small, irregularly lobed and lie within the inner longitudinal muscles. They are arranged in an irregular single row, sometimes so irregular that it appears as two. The long axis of the testes is in a dorso-ventral plane. These glands alone are found within the inner longitudinal muscle layer, for the vitellaria, while having their origin median to the muscles, soon grow between these fasciculi and so extend into the cortical parenchyma (Fig. 73). The testes range in size from 0.060 to 0.108 mm. in length to 0.048 to 0.072 mm. in width. The number in trans-section varies from 8 to 16. The mitotic figures show with almost diagrammatic clearness. The number of testes range from 210 to 225 and was determined by an estimation of their number. The vas deferens is first clearly distinguishable in the region just posterior to the center of the body length. The vas deferens is formed medianly about 1.3 mm. anterior to the cirrus sac. It is formed by the union of three smaller ducts, evidently canals of the *vasa deferentia secundaria*. It is soon crowded ventrally by the coils of the uterus lying anteriorly to the cirrus sac. In toto mounts of the ventral surface the entire region filled with the vas deferens is blocked off as an inverted capital "U." This duct passes posteriorly through numerous convolutions. The diameter of the tube is small and the width varies from 16 to 24  $\mu$ . The testes disappear from the center of the field with the advent of the vas deferens and the uterine coils. However, they still persist laterally, leaving the median 0.2 mm. of the medullary parenchyma to the developing tubes of the reproductive systems. As the cirrus sac is approached the inner longitudinal muscles are pushed nearer the surface thus bowing out the muscles of that region. Shortly before this organ is reached the vas deferens winds medianly and passes into a small narrow ductus ejaculatorius. This canal is surrounded by circular muscles which in turn are surrounded by cells which do not stain as deeply as those about the uterus and so may readily be distinguished from them. The ductus ejaculatorius passes ventrally where it forms a seminal vesicle. This structure is 84  $\mu$  in length and 60  $\mu$  in width. The cavity itself lies in a nearly horizontal plane and is 52 by 14  $\mu$ . Upon leaving the seminal vesicle the ductus ejaculatorius doubles back upon itself towards the middle of the body where it penetrates the median anterior wall of the cirrus sac. Around this entire region are numerous muscle fibers which leave the inner longitudinal muscle band to form an almost unbroken layer of muscles surrounding the muscular cirrus sac and the uterine coils above. The cirrus sac is round and having a diameter of

0.21 to 0.26 mm. The circular muscles are 24 to 36  $\mu$  in thickness and evenly distributed (Fig. 74). Retractable fibers for the withdrawal of the cirrus are also present, although not in great numbers. The limits of the cirrus sac do not extend beyond the inner longitudinal muscles. At this point 30  $\mu$  from the outside, the cirrus sac empties into the middle of the male genital atrium. This atrium is 40  $\mu$  in length and 30  $\mu$  in breadth at the surface. It extends dorsally for 60  $\mu$  surrounding the ventral portion of the cirrus sac; in other words the lower portion of the cirrus sac protrudes into the male genital atrium. The extruding cirrus of the parasite in toto mount gave the following measurements:

length.....	0.30 mm.
width at apex.....	0.072 mm.
width in middle.....	0.108 mm.
width at base.....	0.144 mm.

The apparent discrepancies in measurements between the width of the cirrus and the diameter of the male genital atrium indicates that it is capable of considerable expansion. The female reproductive system opens to the surface in a female genital atrium. The anterior border of this cavity is 30  $\mu$  posterior to the closest edge of the male atrium and the centers of these two cavities lie approximately 60 to 70  $\mu$  behind each other (Fig. 75).

The female reproductive system of *C. singularis* is unusual in several details and therefore is of particular interest. In the first place, the uterus extends anteriorly to the cirrus sac and in the second, the coils do not reach posteriorly beyond the level of the oötype. The position of the vitellaria is also unique. All of these facts coupled with others of lesser importance mark it as one of the most interesting species encountered. The ovary is lobular and is confined to the lateral third of the medullary parenchyma. It is not as long as those of other species, measuring from 0.25 to 0.35 mm.; the maximum width is about 0.19 mm. The ovary extends to the anterior side of the cirrus sac; it assumes an "H" shape with the ovarian commissure exactly in the middle. But this commissure is much weaker than is normally the case for its diameter varies from 24 to 36  $\mu$ .

The oöcapt arises from the posterior ventral margin of the ovarian commissure, slightly to the right of the center. It is 14  $\mu$  wide with circular muscles 2 to 3  $\mu$  thick surrounding this canal for 10 to 12  $\mu$ . The oviduct arising from the distal extremity of the oöcapt is relatively long and measures, not including the oöcapt, 80 to 90  $\mu$ . It passes ventrally and winds to the left just within the boundary of the oötype whose cells permeate this entire region from the ovarian commissure to the post-ovarian vitellaria. The maximum width reached by the oötype is 0.216 mm. This may vary in different specimens but it fills the entire medullary parenchyma dorso-

ventrally, and within its confines are found the vagina, vitelline ducts, oviduct, and the beginnings of the uterus (Fig. 35).

The center of the female genital atrium lies 60 to 70  $\mu$  posterior to that of the male. This atrium only lies 80  $\mu$  anterior to the ovarian commissure. It extends dorsally for 0.115 mm. and at this point it divides into two ducts, one the vagina, passing to the right, and the other the uterus, entering from the left. These ducts empty near the middle of the body (Fig. 75). The vagina is median and soon coils dorsally above the center of the body passing anteriorly and then posteriorly. It shortly forms an arc across the dorsal portion of the anterior edge of the oötype and passes ventrally and to the left where it is joined by the oviduct from below. The vagina does not expand to form a receptaculum seminis. The duct is lined by a thin cuticula-like membrane about which is a layer of circular muscles. These in turn are surrounded by cells, the myoblasts of the muscle layer. The vitellaria are of particular interest for several reasons. In the first place they are very small, measuring from 36 to 60  $\mu$  by 14 to 24  $\mu$ . These glands originate from the medullary parenchyma, but they grow towards the surface. Their general shape, therefore, resembles an Indian club, or a Florence flask, with the smaller neck situated medianly and the bulk of the gland lying outside of, or between, the inner longitudinal muscles. As the vitellaria are small they are present in greater numbers (Fig. 73). This is evident from the toto mounts where as many as 13 to 15 rows may be counted on one surface (Fig. 35). These rows are continuous longitudinally and present an unusual appearance which is characteristic for the species; they connect at the lateral margins with the post-ovarian vitellaria. The vitelline ducts are numerous and lie within the medullary parenchyma. The main ducts are situated laterally for all of the others converge to these two which in turn are joined by those from the post-ovarian vitellaria. These combined vitelline ducts parallel the ovary where they unite medianly to form a single duct. It is this vitellarian canal which penetrates the oötype, passes ventrally, and finally dorsally to unite with the combined vaginal-oviducal canal, or fertilization chamber. In this species this chamber is 50  $\mu$  in length. With the juncture of the common vitelline duct the uterus is formed which soon passes obliquely dorsal and is surrounded with glandular cells as well as circular muscle fibers. The lining of this portion of the canal is unusual for it appears striated with these striations caused by protrusions into the duct. The wall is composed of cells between which empty ducts from the glandular cells. Circular muscle fibers lie scattered between the cells lining the canal while radiating longitudinal muscle fibers are also present. It is probable that the cells lining the canal are glandular and it is evident that those lying at some distance from the canal are also glandular in nature (Fig. 76). The uterus makes several convolutions through



the oötype, turns anteriorly and soon leaves the confines of the oötype. Even before leaving this organ the deep staining glandular cells which typically surround the uterus appear. This canal passes anteriorly keeping a position dorsal to the cirrus sac until beyond it where it becomes more convoluted. The uterus passes 0.36 mm. anterior to the cirrus sac and dorsal to the vas deferens. It has two main branches, the ascending and descending uterine limbs. These may sometimes become so convoluted that three or four portions of the uterus appear in cross section, though always in the dorsal half of the body. The glandular walls of the uterus are found throughout its entire length, the cells even persisting until the duct empties into the female genital atrium. The eggs of this species are small and ovoid. Only a few were present and these varied in size from 40 to 45  $\mu$  in length by 21 to 26  $\mu$  in width.

*Capingens singularis* clearly belongs in the family Caryophyllaeidae and the position of its sexual aperture, ovary and the presence of the uterine glands place this form in either the Capingentinae or Lytocestinae. In view of the extension of the vitellaria past the inner longitudinal muscles and into the cortical parenchyma *C. singularis* clearly goes into the former. There are two other genera in this subfamily, *Pseudolytocestus* Hunter 1929, and *Spartoides* Hunter 1929. The main point of difference between the two is in the type of scolex which in the case of the latter resembles the scolex of *Hypocaryophyllaeus*. The massive scolex of *C. singularis* occupies one-fourth the body length and possesses a deep bothria-like sucker on the dorsal and ventral surfaces. This together with the Caryophyllaeidae-like uterus and the presence of post-ovarian vitellaria clearly separate it from either *Pseudolytocestus* or *Spartoides*. Yet it belongs in this subfamily as was shown above, and the author therefore created a new genus, *Capingens*, to hold this form (Hunter 1927). Originally this genus was placed in Lytocestinae, but was transferred to the Capingentinae on the basis of the vitellaria in relation to the inner longitudinal muscles when this new subfamily was created. It is taken as the type genus of the subfamily.

#### GENUS PSEUDOLYTOCESTUS HUNTER 1929

Generic diagnosis: Capingentinae possessing little specialization of scolex. Cirrus opens separately on ventral surface or into a shallow ever-sible genital atrium. Ovary "H" shaped, almost entirely medullary, only one third of the ovarian follicles extend into cortical parenchyma. Uterine coils never extend anteriorly to cirrus sac, with a maximum length of one third that of testicular field. Post-ovarian vitellaria absent. Parasitic in the intestines of the Catostomidae. Development unknown.

Type and only species: *Pseudolytocestus differtus*, Hunter 1929.

This genus differs from *Monobothrium* primarily in that the vitellaria are not entirely medullary, the cirrus sac does not open via a distinct genital papilla and there are no loculi nor distinct terminal introvert on the scolex. Neither can it be made a synonym for either *Spartoides* or *Capingens*, as the ovary alone in the former and the scolex of the latter would be sufficient to exclude this form from both. Since this form fitted none of the available genera of the *Pseudolytocestinae* it was necessary to create a new genus to hold it. Because of the superficial resemblance of this to the genus *Lytocestus* the new genus is named *Pseudolytocestus*.

*PSEUDOLYTOCESTUS DIFFERTUS* HUNTER 1929

[Figs. 23, 26, 52, 71, 91]

1929: *Pseudolytocestus differtus* Hunter 1929: 188.

Specific diagnosis: With characters of genus. Adult parasites free in intestine, length 10 to 20 mm.; width 0.6 to 1.7 mm. Neck distinct and short, 0.9 to 1.7 mm. long by 0.6 to 0.95 mm. wide. Musculature of scolex generally resembles that of *C. terebrans*. No external longitudinal grooves present. Body broadens posteriorly and is oval in cross section. The cuticula tripartite, outer stainless and tubercular, inner takes eosin, lined with basement membrane; composite 8 to 10  $\mu$  thick. Subcuticula 15 to 20  $\mu$  deep, bounded medianly by the cortical layer of the parenchyma which is 68 to 81  $\mu$  in depth. Cuticular and parenchymal muscle systems present and prominent. Testes number 725 to 775, are roughly oval and have a maximum diameter of 0.13 to 0.2 mm. Cirrus sac and external seminal vesicle form the Greek letter "A," joining dorsally. Cirrus sac forms an angle of less than 30 degrees with the vertical, fills entire medullary parenchyma dorso-ventrally, being 0.2 to 0.5 mm. long. The circular muscles of this organ are weak. Female genital atrium opens on ventral surface 0.27 to 0.3 mm. posterior to the male orifice. Utero-vaginal canal 0.16 to 0.34 mm. long, extending dorsally; uterus empties at middle of body from the right. Vagina proper extends dorsally 0.4 to 0.6 mm. until close to the dorsal layer of the medullary parenchymal muscles. It passes ventrally and does not form a receptaculum seminis. Wings of the ovary are 0.6 to 1.35 mm. long and 0.2 to 0.4 mm. wide; these extend out past the inner longitudinal muscles in same manner as the vitellaria; ovarian commissure entirely medullary, 0.23 to 0.27 mm. in diameter. Vitellaria measure 0.13 to 0.2 mm. in maximum diameter, are very irregular in shape extending past the inner longitudinal muscles into the cortical parenchyma (as in *C. singularis*). Eggs large, ovoid from 58 to 65 by 35 to 40  $\mu$ .

Host: *Ictiobus bubalus*, Tallahatchie River, Mississippi. In intestine.

Type: Slides No. 29.47 in the collection of Dr. Henry B. Ward.



Paratype: Vials and slides in the author's collection No. 651.3-651.5

Host	Locality	Collector	Authority
<i>Ictiobus bubalus</i> (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)

This material was found in only four specimens of *Ictiobus bubalus* examined by Dr. Parke H. Simer at Money, Mississippi and then only three or four individual parasites which were often mixed with other species in each host. One host, for example, contained several hundred *B. giganteum* and only two *P. differtus*.

This parasite possesses a scolex which is clearly demarked from the remainder of the body, being smaller and superficially resembling that of *C. terebrans*. The base is conical and regular and bears no definite indication of loculi or suckers (Fig. 23). Its length varies from 0.6 to 0.95 mm. while the breadth is 0.6 to 0.8 mm. The inner longitudinal muscles forming a terminal introvert are found attached in the region of the basement membrane of the distal extremity of the scolex. The muscles at the point of attachment to the scolex form an oval measuring 0.54 by 0.27 mm. As the inner longitudinal layer passes posteriorly through the scolex the muscles pass laterally so as to increase the area of the medullary parenchyma and in so doing decrease that of the cortical layer. The fasciculi of the inner longitudinal muscles continue as a ring from their insertion on the distal extremity of the scolex and pass posteriorly (Fig. 71). These fasciculi range from 15 to 40  $\mu$  in length and 13 to 15  $\mu$  in width. There are between 20 and 30 large individual fibers in each group. External to the inner longitudinal muscles lies the cortical layer of the parenchyma filled with nuclei and is 68 to 81  $\mu$  in depth and 25 to 30  $\mu$  from the exterior. This layer is bounded externally by the outer longitudinal muscles which are 4 to 6  $\mu$  thick and contain 3 to 6 individual muscle fibers per fasciculus. The subcuticula is relatively thin being only 15 to 20  $\mu$  and but 8 to 10  $\mu$  from the outside. In the outer limits of the subcuticula lie the relatively prominent longitudinal and circular muscles of the cuticular system. The outermost edge of the subcuticula is marked by the basement membrane of the cuticula about 1  $\mu$  thick and contains the circular cuticular muscles. External to this and taking an eosin stain is a smooth layer of material 4 to 5  $\mu$  thick while the outermost layer is but 3 to 4  $\mu$  thick. This latter strip remains impervious to stain but is covered with a number of irregular granular tubercles scattered every

few micra throughout the layer. The neck does not possess any outstanding characteristics, being 0.9 to 1.7 mm. in length and 0.6 to 0.94 mm. in breadth. The excretory tubules are arranged in pairs as in other species. Contrary to many forms the maximum body width which varies from 0.9 to 1.2 mm. at the widest spot occurs just posterior to the neck and not in the region of the reproductive organs. The excretory system first appears in the anterior portion of the scolex where it is composed of the paired ascending and descending tubes. The former unite to form a ring from which the canals of the descending system take their origin. There are usually 10 pairs of main tubes altho some slight variation in this number has been noted. The descending canals terminate in a "T" shaped excretory vesicle located at the posterior tip of the body and varying in length from 0.1 to 0.16 mm. and in width from 0.025 to 0.03 mm. in the stem of the "T" and 0.1 to 0.13 mm. from tip to tip of the cross arms.

The small oval testes number between 725 and 775. This is by far the greatest number encountered and is explained by the relatively small size of these glands, 0.1 to 0.18 mm. long by 0.06 to 0.094 mm. wide (Fig. 91). The testes are arranged in two rows one dorsal to the other. The vitellaria surround them and are not found in the mid-region of the medullary parenchyma. The method used in the determination of the number present varies somewhat from the one typically followed. (Cf. page 11). Twenty testes picked at random were traced through to determine in how many sections they appeared. The average of these was taken and this number was divided into the total number of times that parts of testes were encountered in each section. This number, 4,537, divided by the average section number for each testis, 6, yields our number of 756, the number in this particular specimen. Several others were counted to check this and a second gave 750, and a third 759, so by allowing for variations and possible error we find the actual number is between 725 and 775.

Posteriorly the testes become pushed aside to make room for the coils of the vas deferens. This organ is surrounded throughout its course by a row of vitellaria and in addition it is usually flanked by four or five testes. The vas deferens may be said to occupy the middle third of the body. The maximum diameter of this organ varies from 0.067 to 0.168 mm. Ventrally the vas deferens gives way to the small muscular ductus ejaculatorius 0.04 to 0.06 mm. wide, the layer of surrounding muscles being 0.01 to 0.015 mm. thick. It arises 0.3 to 0.38 mm. anterior to the base of the seminal vesicle. Its path is tortuous, starting close to the ventral inner longitudinal muscles it winds dorsally for about 0.15 mm. and then ventrally for 0.1 mm. and finally dorsally and laterally passing into the lower end of the seminal vesicle. This organ is practically straight and lies in a dorso-ventral plane, forming the left arm of a Greek "A" at an angle

of about 30 degrees from the vertical. It is 0.35 to 0.45 mm. long and 0.15 to 0.2 mm. wide with prominent muscles 0.03 to 0.04 mm. thick. The cavity of the seminal vesicle is from 0.3 to 0.4 mm. by .075 to 0.093 mm. Along the base of the circular muscle layer are scattered cells which are 4.5 to 7.7  $\mu$  long. The seminal vesicle narrows and passes into a continuation of the ductus ejaculatorius which is less than 0.2 mm. long, which in turn passes into the long weakly muscled cirrus sac; this occupies all of the medullary parenchyma dorso-ventrally and one third laterally. It extends slightly posteriad forming the right arm of the Greek "A." The cirrus sac is ovoid being two to two and a half times as long as it is broad; it measures 0.2 to 0.8 mm. by 0.1 to 0.4 mm. (Fig. 26). Contrary to the usual situation the muscles of the cirrus sac are not concentrated along the outer edge and consequently do not form a definite band (Fig. 52). The distal extremity of the cirrus sac when extruded forms an irregular serrated margin thus resembling the genus *Monobothrium* (Fig. 52).

The female reproductive system usually opens on the surface or more rarely into a shallow atrium 33 to 67  $\mu$  deep. The utero-vaginal canal extending dorsally for 0.13 to 0.27 mm. is close to the middle of the body. The uterus empties from the right at this point while the vagina continues dorsally until 0.4 to 0.6 mm. above the ventral surface. It then dips towards the ventral surface and passes posteriorly, keeping close to the ventral inner longitudinal muscles until the ovarian commissure is reached; the vagina passes up over this without forming a receptaculum seminis, dips ventrally and enters the oötype complex where it joins the oviduct to form the fertilization chamber.

The vitellaria are very irregular in shape for they extend past the inner longitudinal muscles much as they do in *C. singularis* (Fig. 91). Some few vitellaria may be found entirely external to this muscle layer while one or two are occasionally found entirely internal to it. The bulk of these glands, however, originate within the inner longitudinal muscles and push their way out past this layer to extrude for nearly one half their length into the cortical parenchyma (Fig. 91). The size varies from 0.08 to 0.17 mm. and 0.05 to 0.1 mm., being thinnest where they are squeezed between the inner longitudinal muscles. These glands entirely surround the testes and form a definite layer. The two vitelline ducts appear near the median lateral group of glands and pass posteriorly towards the ovary. Here they pass mediad to the ovarian wings, pass dorsally over the ovarian commissure where these two ducts turn medianly, join, and after nearly 0.2 mm. join the fertilization chamber. There are no post-ovarian vitellaria. (Figs. 26, 52.)

The ovary is a very prominent structure, "H" shaped, but with the lower arms longer and slightly narrower than the upper. The formation is follicular, each follicle being connected by a thin stem to the main com-



missure (Fig. 26). This is also characteristic of *C. singularis*, to which it appears related in several other respects. The wings reach within 0.5 mm. of the posterior tip and measure 0.6 to 1.8 mm. long and 0.13 to 0.27 mm. wide, while the commissure has a maximum diameter of 0.23 to 0.27 mm. The oviduct arises at the median posterior edge of the commissure where an inconspicuous oöcapt is formed. The oviduct passes posteriorly for 60 to 75  $\mu$  and is joined by the vagina. The fertilization chamber thus formed is about 100  $\mu$  long at whose termination the vitelline duct empties and the uterus is formed. Contrary to the usual method of procedure this limb of the uterus passes dorsally and remains in this position until opposite the posterior tips of the ovarian wings. Here the uterus dips ventrally and passes anteriorly; it also becomes surrounded by uterine glands and the cavity becomes somewhat wider. The uterus crosses the ovarian commissure in the middle of the body and becomes more coiled as it passes anteriorly. The coils do not pass the posterior limits of the cirrus sac. The last 0.5 mm. of the uterus is lined with a thin layer of circular muscles instead of the usual uterine glands. The eggs are ovoid and are 60 to 68 by 35 to 42  $\mu$ , averaging 63 by 38  $\mu$  in size.

*Pseudolytocestus differtus* differs from all of the other species of the subfamily Capingentinae. Both *Capingens singularis* and *Spartoides wardi* have fewer testes, being 210 to 225 and 65 to 105 respectively compared with 725 to 775 in *P. differtus*. The scolex of *C. singularis* and the ovary of *S. wardi* are sufficient characters in themselves to distinguish them from ever being more closely associated than members of the same subfamily. At first glance *P. differtus* appears to belong in the genus *Monobothrium*. A more careful study shows a number of differences which are valid. First one notes the location of the vitellaria in relation to the inner longitudinal muscles. A glance at the sections show the dearth of longitudinal grooves on the scolex of *P. differtus* with but doubtful indications of the existence of a terminal introvert. Further, every specimen of *M. ingens* examined possessed a cirrus which was extruded thru a bulky annular pad (Fig. 39), while the typical picture of *P. differtus* occurs in figure 52. In only one instance was the cirrus found extruded in the latter species and then the whole outer edge was serrate and not papillate as in *Monobothrium*. These are sufficient grounds to maintain this form in the new genus *Pseudolytocestus*. The specific name "*differtus*" was given to indicate the crowded nature of the parenchyma of this parasite.

#### GENUS SPARTOIDES HUNTER 1929

Generic diagnosis: Capingentinae possessing three pairs of loculi on a distinct scolex. Male and female pores open separately on ventral surface near posterior tip of the last fourth of the body. Cirrus sac opens within the confines of the ovarian wings. One row of main longitudinal

muscles; vitellaria and ovarian follicles are in part cortical to the inner longitudinal muscles; ovarian commissure entirely medullary. Ovary "U" shaped, uterine coils extending anteriorly to the cirrus sac more than twice the length of the ovarian wings. Post-ovarian vitellaria absent. Parasitic in the Catostomidae. Development unknown.

Type and only species: *Spartoides wardi*, Hunter 1929.

This genus was placed in the Capingentinae primarily because of the relation of the vitellaria and ovarian wings to the inner longitudinal muscles. The members of this genus differ from all the others in the shape of the ovary which is like the capital letter "U". This is a marked difference from the characteristic "H" shape of so many of the Caryophyllaeidae, the only other occurring in the genus Caryophyllaeides, Nybelin. This latter genus possesses an ovary with the shape of an inverted capital "A", and is composed of two species, *C. fennica* (Schneider 1902) and *C. skrjabini* (Popoff 1924). In *Spartoides* the uterine coils extend anterior to the cirrus sac which has the unique distinction of lying within the ovarian wings at the anterior margin of the ovarian commissure. Further the uterine coils lie almost exclusively anterior to the cirrus sac. The genus was so named because of its great length and thinness thereby resembling a thread.

*SPARTOIDES WARDI* HUNTER 1929

[Figs. 13, 14, 28, 61-63, 86-89]

1929: *Spartoides wardi* Hunter 1929: 188-189.

Specific diagnosis: With the characters of the genus. Adult parasite 8 to 30 mm. by 0.3 to 0.7 mm. Neck distinct, ranging from 1.6 to 4.7 mm. by 0.2 to 0.55 mm. Maximum body width exclusive of the scolex 0.5 mm. Body oval in cross section; cuticula 2 to 3  $\mu$  in thickness; subcuticula and cortical parenchyma indistinguishable, 42 to 58  $\mu$  thick. Inner longitudinal muscles present and prominent; outer longitudinal muscles fused with longitudinal cuticular muscles. Testes number 65 to 105, usually appear two per section, and have a maximum diameter of 0.13 to 0.2 mm. Cirrus sac oval to triangular, occupying nearly all of medullary parenchyma; maximum diameter 0.09 to 0.14 mm., circular muscles thin, 9 to 12  $\mu$  in width. Seminal vesicle prominent, 0.13 mm. in length, the circular muscles 30 to 45  $\mu$  thick. Male and female reproductive systems open on the surface 60 to 85  $\mu$  apart. Vagina very short and straight, not forming a receptaculum seminis, but extending dorsally to join the combined ovi and vitelline ducts almost immediately. Vitellaria take their origin in the medullary parenchyma but extend past the inner longitudinal muscles into the cortical parenchyma; smaller than the testes and are 0.1 to 0.15 mm. in maximum diameter. Six pairs of main excretory canals appear in cross section, terminating in typical excretory vesicle. Eggs ovoid 42 to 54 by 22 to 27  $\mu$ .



Host: *Carpiodes carpio*, Rock and Mississippi Rivers, Illinois and Iowa; *Carpiodes thompsoni*, Lake Pepin (Mississippi River), Minnesota; *Ictiobus cyprinella*, Rock River and Lake Pepin (Mississippi River), Minnesota. In intestine.

Type: Slide No. 29.48 in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology University of Minnesota. Slides and vials Nos. 420, 425, 408, 470.1 and 500 in the collection of the author.

The material furnishing the basis for the description of this parasite was taken during the fall of 1924 and the summers of 1925 and 1926. Dr. J. F. Müller collected this form in 1924; Essex and Hunter (1926) gave a general account of the collections of 1925 and the author personally collected many samples of this form while working at the U. S. Fisheries Biological Station at Fairport, Iowa the following year (1926). This parasite was readily distinguishable by its unusual length and thinness which was unique among the forms encountered by the author. Likewise it was collected with greater frequency than many of the other species.

Host	Locality	Collector	Authority
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
<i>Ictiobus cyprinella</i> (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
<i>Carpiodes thompsoni</i> Agassiz	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
<i>Carpiodes carpio</i> (Rafinesque)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
<i>Carpiodes carpio</i> (Rafinesque)	Rock River, Sterling and Rock Falls, Ill.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
<i>Carpiodes carpio</i> (Rafinesque)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)

*Spartoides wardi* is a very long, thin and narrow parasite; the adults measure 8 to 30 mm. in preserved material while the living specimens reach nearly 50 mm. Usually the adults are from 15 to 50 mm. in length, and the width varies from 0.3 to 0.7 mm. The greatest width appears in the scolex, but in general *S. wardi* presents an unusually monotonous appearance. The neck is long and thin and the vitellaria extend for some distance anteriorly to the testes. The uterine coils and ovary are distinct

while the cirrus sac and seminal vesicle are less sharply defined than usual. The scolex of *S. wardi* is quite prominent and in side view appears wedge shaped (Fig. 13). It varies from 0.2 to 0.54 mm. in length and from 0.5 to 0.67 mm. in breadth. The widest area occurs at the base of the scolex while the distal portion is gently rounded in a typically preserved form. The scolex may take a variety of forms since this organ is very active. Viewing the scolex from the dorsal and ventral surfaces there appear to be two lappets in which are embedded many of the fibers of the inner longitudinal muscles (Fig. 14). These lie between the three weak sucking grooves and may be extended or withdrawn. The action of the scolex is interesting when observed on living material. At rest the scolex appears three pointed or pronged with the median projection extending twice as far anteriorly as the two which flank it. As most of the inner longitudinal muscles are attached to the region between the two side lappets and the central one it keeps the demarkation distinct. The next phase of the movement consists in a drawing in of the median projection and a corresponding bellying out and expansion of the two lateral lappets until all three are of equal size. The last phase is a continuation of the roll of the side lappets until they in turn extend farther anteriorly than the central one. With an extension of the central cone again we have the first position reached. This movement is aided by the flow of the fluid in the excretory canals and particularly the ring clearly seen in figure 62.

In cross section the scolex shows but slight evidences of specialization. The surface is broken on the dorsal and ventral surfaces by three pairs of loculi or bothria (Fig. 61). These are poorly defined and show practically no specialization for adhesion. The inner longitudinal muscles are grouped into eight fasciculi which are connected to each other by scattered fibers; there are from ten to twenty-five fibers in each fasciculus. A few canals of the excretory system can be seen in the more distal portions of the scolex. These are fine and scattered (Fig. 61). As the base of the scolex is approached the inner longitudinal muscles become more definitely separated into eight distinct groups and the irregular collecting ring of the excretory system begins to show clearly (Figs. 62, 89). The two ducts of the ascending canals lie in the medullary parenchyma while outside these appear the wide thin-walled canals of the descending system. The ascending ducts are found to take their origin from those lying next the descending canals of the excretory system in the cortical parenchyma. As the scolex is reached each pair of the canals fuse in the medullary parenchyma to form one (Fig. 62). These may be later reduced; they extend to the more distal portions of the scolex and then turn sharply towards the cortical region where they are absorbed in the collection ring in the lower regions of the scolex. From this ring the six descending canals take their origin. These pass posteriorly and in the lower neck region are joined by

the ascending canals so that the typical paired excretory canals appear in the cortical parenchyma. These descending canals empty posteriorly into the excretory vesicle near the posterior tip of the body. The ascending canals soon pass into the glandular region of the neck after penetrating the medullary parenchyma. The function of these glands is unknown.

The cuticula of this parasite is very thin, measuring from 2 to 3  $\mu$ . The cuticula is followed immediately by the thin circular cuticular muscles which are less than 1  $\mu$  in thickness. This layer is followed by a clear distinct layer of longitudinal muscles; these probably represent the combined cuticular and outer longitudinal muscle layer as they are more prominent than either of these would be alone. Owing to their position they are considered as cuticular longitudinal muscles (Fig. 63). They have a maximum number of 2 or 3 per fasciculus but usually appear singly, and measure 3  $\mu$  in cross sections. The subcuticula, because of the apparent absence of the outer longitudinal muscles, is combined with the cortical layer of the parenchyma. As it varies in thickness from 42 to 58  $\mu$  and contains not only the paired ducts of the excretory system but also the nuclei so often confined to the subcuticula.

The male reproductive system is unique in some respects and differs from those heretofore encountered. The testes are large, irregularly ovoid to spherical and measure 0.13 to 0.2 mm. in maximum diameter; they number between 65 and 105. Owing to their size there are but two or more rarely three testes visible in cross section (Fig. 63). Typically one finds a dorsal and ventral testis in section flanked dorso-ventrally by the inner longitudinal muscles and laterally by two or three vitellaria. The testes give rise posteriorly to a small vas deferens situated medianly. This duct expands as the last vitellaria are passed and winds posteriorly keeping ventral to the coils of the uterus (Fig. 28). The path is decidedly tortuous until the ovarian wings are reached when the course of the vas deferens becomes straighter even tho it lies ventrad to the ovarian wings for the greater part of its course (Fig. 28). Soon after passing the anterior half of the ovarian wings the vas deferens becomes narrower and more thick walled to form the ductus ejaculatorius. This canal is greatly curved and enters the seminal vesicle near the mid ventral surface (Fig. 88). The seminal vesicle is situated well between the wings of the ovary and in the case of heavily contracted forms it lies beneath the ovarian commissure. (Figs. 28, 88.) This vesicle is larger than the cirrus sac, oval and highly muscular. It is 0.13 mm. long; the circular muscles 27 to 45  $\mu$  in thickness, surround a cavity having a diameter of 70 to 75  $\mu$ . The seminal vesicle lies dorsal to the cirrus sac and empties into it from above via a short continuation of the ductus ejaculatorius which is 0.06 to 0.12 mm. long and is surrounded by a lining 2 to 3  $\mu$  in thickness which in turn is covered by a layer of circular muscles about 12  $\mu$  across. The cirrus sac appears roughly triangular in shape and is



surrounded by circular muscles from 9 to 12  $\mu$  thick, the maximum diameter of the cirrus sac is from 0.09 to 0.14 mm. It lies ventral to the ovarian commissure and sometimes slightly anterior to it (Figs. 28, 88). The cirrus opens to the outside about 0.5 mm. from the posterior tip of the body. In one case the cirrus was found extruded from the body and measured 45  $\mu$  in length by 18  $\mu$  in diameter (Fig. 88). The male and female reproductive systems open on the surface 60 to 85  $\mu$  apart (Fig. 28).

The female reproductive system has the most unique arrangement yet encountered. The vitellaria are arranged in two lateral rows and so do not surround the testes. They are irregular in shape and are darker and smaller than the testes, measuring 0.1 to 0.14 mm. in diameter. Some of these glands extend past the inner longitudinal muscles as in the case of *Capingens singularis* and *Pseudolytocestus differtus* and so take a more irregular shape than usual (Fig. 63). They are drained by two small vitelline ducts lying mediad to the vitellaria and between them and the testes (Fig. 63). These ducts fuse ventrally to the ovarian commissure to form the common vitelline duct (Fig. 87). There are no post-ovarian vitellaria, the area behind the ovary being filled by the oötype and coils of uterus.

The shape of the ovary is different from any Caryophyllaeidae yet studied, being the shape of a capital "U". It measures 0.4 to 1.2 mm. in length, 0.2 to 0.4 mm. deep and 0.09 to 0.18 mm. broad. Fourth-fifths of the ovary lies anteriorly to the cirrus sac. The follicular ovary lies externally to the inner longitudinal muscles, thus making the follicles cortical rather than medullary as is typically the case. In fact nearly one half of the ovarian wings lie in the cortical parenchyma (Figs. 28, 86). Another peculiarity of this gland lies in the fact that in cross section it appears nearly circular. Ventrally there is a slight break and at the ends a slight lateral turning of the glands which suggests at once the capital Greek letter "Ω" (Fig. 86). The ovarian commissure is quite thick and varies in diameter from 0.13 to 0.18 mm. The oöcapt arises from the median posterior ventral surface of the ovarian commissure. It is fairly well developed, the duct being 8 to 10  $\mu$  wide surrounded by muscles on each side to the depth of 8  $\mu$  (Fig. 87). In this species the oöcapt gives rise to a short oviduct which has a maximum length of 50  $\mu$  before it is joined by the vagina. The oviduct is surrounded throughout its path by a thin layer of circular muscles. The vagina in this species is the shortest yet encountered. It arises as a dorsal continuation of the utero-vaginal canal and its commencement is marked by a small sphincter muscle which occurs at the point of juncture with the uterus (Fig. 87). The vagina extends dorsally for about 0.15 mm. and then turns anteriorly. It joins the oviduct and forms the fertilization chamber, or the vaginal-oviducal canal. This portion is not wider than the vagina proper which has a diameter of 10 to 15  $\mu$ . Close to the union of this canal the inconspicuous common vitelline duct empties while the vagina continues almost straight dorsad (Fig. 87). As it reaches the medullary parenchyma it dips

and passes posteriorly to the ovarian commissure entering the oötype proper. Throughout its length the duct is surrounded by a few circular muscle fibers. The oötype is small and the uterus soon leaves the confines of this gland and after several convolutions passes anteriorly dorsal and lateral to the ovarian commissure (Figs. 28, 87, 88). As the ovarian commissure is approached the typical uterine glands appear and are in evidence until within 0.3 mm. or less of the outside. The coils of the uterus are complicated, extending both dorsally and laterally within the confines of the inner longitudinal muscles. When the testes are reached the uterus doubles back upon itself towards the female pore. These coils have a longitudinal extent of between one fourth and one third that of the testicular field; usually about one fourth. Posteriorly the uterus becomes thin walled, passes ventrally to the ovarian commissure and joins the vagina to form the utero-vaginal canal. This is 40 to 60  $\mu$  in length and lies but a scant 0.3 mm. from the posterior tip of the body surrounded by a continuation of the cuticula the latter in turn being surrounded by a number of clear cells (Fig. 87). The eggs are ovoid and measure 45 to 54 by 22 to 27  $\mu$ .

This parasite clearly belongs in the genus *Spartoides* on the basis of all the characters and as it is the only species so far described there are no comparisons to be made with other forms. From the beginning it is set aside by the peculiar shape of the ovary as well as the arrangement of the reproductive systems. It is named in honor of that great American teacher of parasitology, Dr. Henry B. Ward, head of the Department of Zoology of the University of Illinois.

#### SUBFAMILY WENYONINA E Hunter 1927

Subfamily diagnosis: Caryophyllaeidae in which the sexual apertures are situated in anterior half of the body. Ovary is situated in posterior body half. Longitudinal muscles may consist of either one thick layer occupying entire cortex or this may be split into two layers resembling those of the Lytocestinae. Vitellaria medullary, confined to two lateral rows. Uterine glands absent.

Type and at present only genus: *Wenyonia* Woodland, 1923.

#### GENUS WENYONIA WOODLAND 1923

Generic diagnosis: Wenyoninae in which scolex may or may not be specialized. The longitudinal extent of uterus is at least equal to that of testicular field. Ovary medullary, follicular and "H" shaped. Ovarian commissure not reduced, terminal excretory bladder present. Parasitic in Siluridae. Development unknown.

Type species: *Wenyonia virilis* Woodland, 1923.

To include:

- (1) *W. virilis* Woodland 1923.
- (2) *W. acuminata* Woodland 1923.
- (3) *W. minuata* Woodland 1923.



## MORPHOLOGICAL DATA

## GROWTH IN LENGTH IN CESTODARIA

It is known that some Cestodarian parasites are less than 0.5 mm. in length when they reach the digestive tract of their definitive host, and that such may grow to be 14 times their original size. In larger species which range from 70 to 80 mm. the increase in size would be 140 to 160 times. The growth appears in the region of the body posterior to and including the first vitellarium. A study has been made of this region of localized growth. The material at hand in several species is remarkably well adapted for such a study, because of the numerous worms, varying in size.

Such regional growth is more readily traced in other groups. The distomes, for example, form an excellent group for such observations. Braun (1894:567) notes that regional growth exists. Von Linstow (1890) working with *Distomum cylindraceum* noted a greater increase in length than width. His data, however, could scarcely be called significant, for he measured only three specimens. Other workers who noted such changes were Thomas (1883) and Leuckart (1886) in *Fasciola hepatica*. Barlow (1923) in measurements of several hundred specimens of *Fasciolopsis buski* finds an interesting though not significant change in proportions. Cort (1921) noted variations in body proportions of *Schistosoma japonicum* which closely parallels the changes described by Manter (1926) for *Otodistomum cestoides*. Ward (1910) notes growth changes for *Azygia sebago*. Here he finds that "The anterior region assumes the form of an ellipse surrounding the two suckers. This region changes relatively little in size with growth. In one of the smallest specimens (measuring 1.6 mm.) the distance between the centers of the two suckers was 0.5 mm. In one 10 mm. long, this distance measured 1.0 mm." Mühlenschlag (1914) in working on *O. veliporum* found that the ratio between the neck region and the body region was 1:4 in young forms and 1:7.8 in the largest adult. He concludes "dass bei verschiedener Grösse der Tierre der Hinterkörper relativ viel stärker wächst der Vorderkörper."

As far as the writer is able to determine there is no data on growth in length in the Cestodaria. The significance of the initial work in this field may be great, and doubly so if the findings corroborate the results of the workers in other fields. An excellent opportunity was afforded the author for the study of the growth in length upon live Cestodarian material. Specimens were secured from *Carpiodes carpio* in considerable quantities. A microscopic examination of the specimens revealed the presence of the

same species in considerable numbers. The parasites were picked over and identifications made. Measurements of the living material were made and then later made into a table (Table I). By placing the specimens under a cover slip with plenty of water little distortion occurred and they could be measured in an extended condition. Measurements on 26 living specimens were obtained in this fashion. From these parasites which measured from 0.65 to 6.53 mm. several interesting correlations were obtained. Perhaps the most significant is that there is a definite ratio between the distance from the anterior tip of the scolex to the anterior side of the first vitellarium, and from that to the posterior tip of the body. In other words, as the parasite grows in length the portion of the body posterior to the first vitellarium increases more rapidly than the region anterior to it (i. e., the neck). The ratio of the differences increases from 1:1.16 in the specimen 0.65 mm. in length to 1:2.53 in the parasite of over 6.5 mm. This latter one

TABLE I

MEASUREMENTS OF HYPOCARYOPHYLLAEUS PARATARIUS BASED ON LIVE MATERIAL

Total length	Mm. to first vitellarium	Mm. from first vitellarium to posterior tip	Difference in mm.	Ratio
1 0.658 mm.	0.304 mm.	0.354 mm.	0.05 mm.	1:1.16
2 0.845	0.436	0.504	0.098	1:1.24
3 1.132	0.404	0.668	0.204	1:1.43
4 1.467	0.598	0.869	0.271	1:1.45
5 1.868	0.778	1.090	0.312	1:1.40
6 1.888	0.744	1.144	0.400	1:1.55
7 2.112	0.802	1.310	0.508	1:1.63
8 2.124	0.802	1.322	0.520	1:1.64
9 2.342	0.882	1.460	0.578	1:1.65
10 2.549	0.952	1.597	0.645	1:1.67
11 2.668	0.992	1.676	0.684	1:1.68
12 2.945	1.100	1.845	0.745	1:1.67
13 3.042	1.132	1.910	0.778	1:1.68
14 3.125	1.175	1.950	0.775	1:1.69
15 3.327	1.200	2.127	0.927	1:1.77
16 3.499	1.234	2.265	1.031	1:1.83
17 3.522	1.290	2.232	1.042	1:1.80
18 3.666	1.300	2.366	1.066	1:1.82
19 3.922	1.360	2.662	1.302	1:1.95
20 4.200	1.400	2.800	1.400	1:2.00
21 4.529	1.436	3.093	1.657	1:2.15
22 4.720	1.496	3.224	1.828	1:2.22
23 5.000	1.600	3.400	1.800	1:2.12
24 5.520	1.700	3.820	2.120	1:2.24
25 6.014	1.840	4.174	2.334	1:2.27
26 6.536	1.850	4.686	2.836	1:2.53

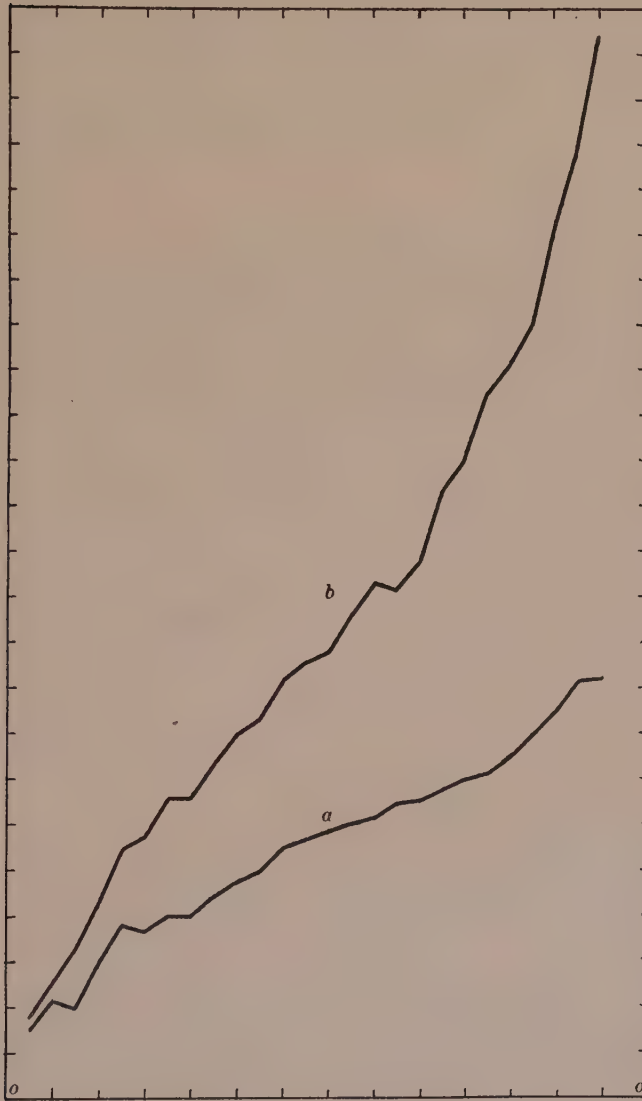


Chart 1. Graphic representation of growth in length in 26 *Hypocaryophyllaeus paratarius*. The base line (0) represents the anterior ends of the parasites while the upper line (b) shows the posterior end of the parasites. The middle line (a) represents the anterior margin of the first vitellarium. Two individuals are indicated between successive vertical lines. Each horizontal line represents two tenths (0.2) of a millimeter.

is sexually mature although the eggs were not present in the uterus in great numbers. This ratio was obtained by dividing the distance to the first vitellarium into the distance from the first vitellarium to the posterior body tip (See Table I). Chart 1 shows this graphically. Here the base line (0) represents the anterior ends of the parasites and the upper curve represents the posterior tip of the body while the middle line marks the anterior edge of the first vitellarium.

#### GROWTH IN LENGTH IN *GLARIDACRIS CONFUSUS*

After studying growth in length on living specimens the writer decided to attempt a similar study upon preserved material. The collections were gone over and the vials containing young forms were run into glycerine and those bearing superficial resemblances were then stained and studied again in cedar wood oil. Thus it was possible to eliminate all but one species, and measurements on 106 of this species were taken. In all cases the measurements were made from the distal tip of the scolex to the most anterior vitellarium and from the anterior edge of this to the posterior extremity. In cases of several of the youngest specimens where differentiation had not clearly occurred the distance from the scolex tip to the most anterior portion of the dark staining-medullary cells, (the anlagen of the vitellaria and testes), was taken. It was found that the total length varied from 0.53 to 20.90 mm. in the 106 individuals. Furthermore, the ratios of the differences ranged from 1:24 up to 1:17.17 in the largest forms studied. This change is of course much more significant than that noted for *H. paratarius* and the study of these data covers more forms and consequently are of greater significance from the statistical standpoint.

After tabulating the measurements an analysis was made of the data and it was found that the parasites fell into seven classes. Class I consists of the individuals whose measurements from the scolex to the first vitellarium were from 0.11 to 0.2 mm., Class II, 0.21 and 0.3 mm., etc. to Class VII, 0.71 mm. and up. Table III shows this very clearly and gives a summary of the data appearing in Table II which includes all of the measurements. Clearly there is a much greater increase in distance from the first vitellarium to the posterior tip than there is from the scolex to the first vitellarium. It should be noted that the maximum measurements in each class show a very definite increase, with the possible exception of Class V. The maximum length for the posterior body portion is only 3.40 mm. while in the preceding class we find it to be 4.44 mm. This is doubtless due to unusual expansion, for the minimum for Class IV is 0.81 mm. compared with 1.23 mm. for Class V, showing a significant increase. The minimum records are perhaps more noteworthy since they probably represent the maximum contraction in each group. Chart 2 gives a graphic representation of these measurements.



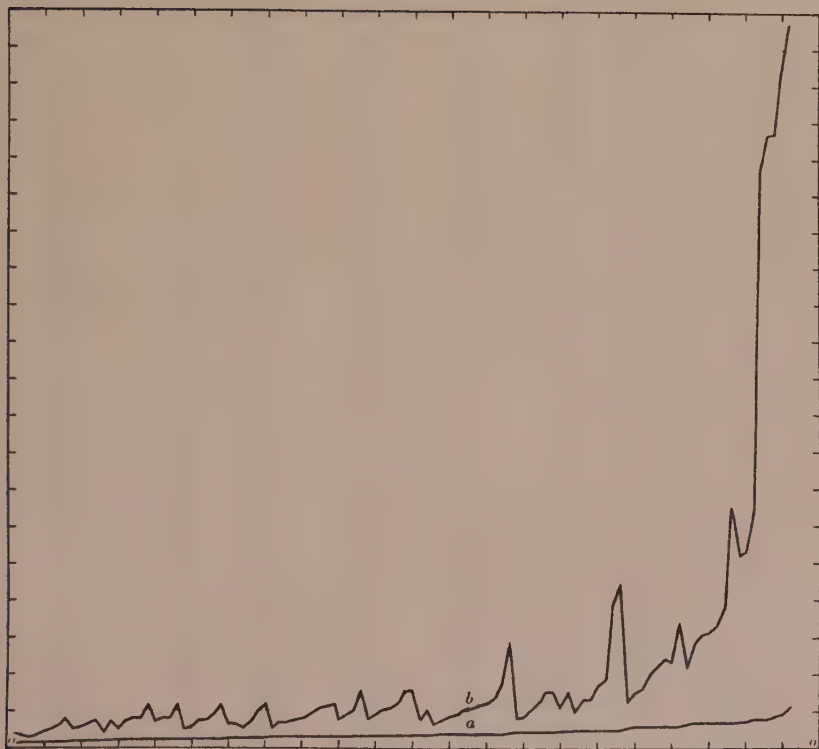


Chart 2. Graphic representation of growth in length in 106 *Glaridacris confusus*. The base line (0) shows the anterior ends of the parasites while the upper line (b) represents their posterior extremities. The middle line (a) indicates the anterior margin of the first vitellarium. Five individuals are represented between successive vertical lines. Each horizontal line indicates one (1) millimeter.

TABLE II  
MEASUREMENTS OF 106 GLARIDACRIS CONFUSUS SHOWING VARIATIONS  
IN LENGTH WITHIN THE DIFFERENT CLASSES

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitel- larium to posterior body tip	Total length
I	1	0.12 mm.	0.41 mm.	0.53 mm.
	2	.15	.38	.53
	3	.15	.30	.45
	4	.15	.35	.50
	5	.17	.46	.63
	6	.17	.51	.68
	7	.17	.61	.78
	8	.17	.81	.98
	9	.18	.51	.69
	10	.18	.56	.74
	11	.18	.66	.84
	12	.18	.76	.94
	13	.20	.41	.61
	14	.20	.76	.96
II	15	.22	.51	.73
	16	.22	.76	.98
	17	.22	.81	1.03
	18	.22	.81	1.03
	19	.22	1.13	1.35
	20	.23	.71	.94
	21	.23	.81	1.04
	22	.23	.91	1.14
	23	.23	1.18	1.41
	24	.25	.51	.76
	25	.25	.58	.83
	26	.25	.74	.99
	27	.25	.76	1.01
	28	.25	.91	1.16
	29	.25	1.13	1.38
	30	.27	.64	.91
	31	.27	.66	.93
	32	.28	.56	.94
	33	.28	.71	.99
	34	.28	1.03	1.31
	35	.28	1.20	1.48
	36	.30	.56	.86
	37	.30	.71	1.01
	38	.30	.71	1.01
	39	.30	.76	1.06
	40	.30	.81	1.11
	41	.30	.96	1.26
	42	.30	1.08	1.38
	43	.30	1.13	1.43
	44	.30	1.18	1.48

TABLE II  
(Continued)

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior body tip	Total length
III	45	0.31 mm.	0.79 mm.	1.10 mm.
	46	.32	.91	1.23
	47	.33	1.03	1.36
	48	.34	1.54	1.88
	49	.35	.79	1.14
	50	.35	.91	1.26
	51	.35	1.05	1.40
	52	.35	1.10	1.45
	53	.35	1.23	1.58
	54	.35	1.54	1.89
	55	.35	1.59	1.94
	56	.38	.77	1.15
	57	.39	1.06	1.45
	58	.40	.67	1.07
	59	.40	.76	1.16
	60	.40	.82	1.22
	61	.40	.92	1.32
	62	.40	1.04	1.44
	63	.40	1.09	1.49
	64	.40	1.19	1.59
	65	.40	1.24	1.64
	66	.40	1.35	1.75
	67	.40	1.74	2.15
IV	68	.44	2.85	3.29
	69	.46	.81	1.27
	70	.46	.86	1.32
	71	.46	1.03	1.49
	72	.46	1.28	1.74
	73	.46	1.64	2.10
	74	.46	1.64	2.10
	75	.48	1.18	1.66
	76	.49	1.64	2.13
	77	.50	1.04	1.54
	78	.50	1.34	1.84
	79	.50	1.34	1.84
	80	.50	1.70	2.20
	81	.50	1.84	2.35
	82	.50	3.91	4.41
	83	.50	4.44	4.94
V	84	.56	1.23	1.79
	85	.60	1.55	2.15
	86	.60	1.60	2.20
	87	.60	2.07	2.67
	88	.60	2.27	2.87
	89	.60	2.93	3.53

TABLE II  
(Continued)

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior body tip	Total length
VI	90	.60 mm.	2.88 mm.	3.48 mm.
	91	.60	3.40	4.00
	92	.66	2.21	2.87
	93	.70	2.88	3.58
	94	.70	3.10	3.80
	95	.70	3.15	3.85
	96	.70	3.30	4.00
	97	.70	3.81	4.51
	98	.70	6.50	7.20
	99	0.76	5.25	6.01
VII	100	.76	5.36	6.12
	101	.80	6.41	7.21
	102	.80	15.65	16.46
	103	.81	16.70	17.51
	104	.89	16.72	17.61
	105	.98	18.5	19.48
	106	1.15	19.75	20.90

TABLE III

SUMMARY OF MEASUREMENTS ON GROWTH IN LENGTH IN GLARIDACRIS CONFUSUS

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior extremity	Total Min.    Max.
I	14	0.12-0.2 mm.	0.3 -0.81 mm.	0.45-0.98 mm.
II	30	0.22-0.3 mm.	0.51-1.20 mm.	0.73-1.48 mm.
III	23	0.31-0.4 mm.	0.67-1.74 mm.	1.07-2.15 mm.
IV	16	0.46-0.5 mm.	0.81-4.44 mm.	1.27-4.94 mm.
V	8	0.56-0.6 mm.	1.23-3.40 mm.	1.79-4.00 mm.
VI	7	0.66-0.7 mm.	2.21-6.50 mm.	2.87-7.20 mm.
VII	8	0.76-up	5.25-19.75 mm.	6.01-20.90 mm.

The matter of growth in length has several interesting angles. In the first place it brings the Cestodaria in line with the trematodes to the extent of showing that the greatest development in both groups occurs in the posterior body region and back of a definite organ. The author does not intend to intimate that any homology exists between these two groups, but simply an analogous type of growth. Even more striking is the comparison with the cestodes. Here are two types of individuals essentially similar, both possessing a scolex, undifferentiated neck, and the body proper containing



the reproductive organs. In the cestodes it is a well known fact that the region of growth lies at the neck and that proglottids are budded off posteriorly with the oldest proglottid lying at the distal extremity. Do we not have evidence of an essentially identical phenomenon here? The region of growth lies, to all intents and purposes, in the neck, for it is this region, and the portion of the body just posterior to it, which shows the greatest changes. The measurements of the length of scolices and necks do not change materially between the young and adult stages, but the body measurements do change corresponding to the proglottids of the cestodes, and the bulk of the growth occurs in this region. This is particularly true of some of the Pseudophyllideans. *Clestopothrium crassiceps* and *Abothrium crassum*, for example, both show this well, as do other forms. In the case of *A. crassum* a young plerocercoid larva, measuring slightly over 0.5 mm. in length had a scolex between 0.025 and 0.03 mm. long, while an older strobila with a length of nearly 3 mm. had a scolex measuring the same or less than that of the plerocercoid just over 0.5 mm. in length. This example serves to show that these, as the Cestodaria, do not undergo any appreciable increase of scolex length. In both these groups the neck does not show any remarkable differences of changes in proportion. This difficulty in measuring neck distances in plerocercoid larvae of the Pseudophyllidea lies in the fact that in the earliest forms differentiation does not occur. *A. crassum*, however, may once again serve as an example. Here the neck, as determined by the distance from the base of the scolex to the first proglottid, varies between 0.2 and 0.4 mm. in specimens which range in size from slightly under 2 mm. to over 8 mm. It is evident therefore, since this species reaches a maximum length of 870 mm. (Cooper 1919:187) that the bulk of the growth occurs posterior to the neck region. In other words the regions which contain the reproductive organs in both the Pseudophyllidea and the Cestodaria are the localities which show the greatest growth. It is evident that the neck region in the Cestodaria as in the cestodes is the region of growth.

The data on growth in length is of further significance in that it points to the danger of basing data on incomplete measurements. For unless minimum and maximum length measurements, etc. are made it may be possible to confuse species. And, whenever possible, the measurements of organs, organ systems, etc. should include minimum and maximum measurements based upon as many different individuals as are available.

#### LIFE HISTORY STUDIES

The original purpose of this monograph was to elucidate the life history of various Cestodaria. Some work had been done in the past by a few European workers. A survey of the literature reveals that the generally accepted theory concerning the life history of the Caryophyllaeidae is essentially as follows: The egg or larva reaches the digestive tract of a

Tubificid worm and then bores through to the body cavity. At this stage it may possess a caudal vesicle (like *Archigetes sieboldi*). After undergoing a certain amount of development the worm is eaten by the definitive host (a fish); upon reaching the digestive tract of the fish the caudal vesicle of the parasite is lost and it becomes sexually mature. D'Udekem (1855) was the first to find such a "larval form" in *Tubifex rivulorum* and *Nais proboscoidea*. According to Nybelin (1922) this form resembles the scolex of *C. laticeps* rather closely. Two other forms also possess marked resemblances to this parasite, Ratzel's (1868) "*C. appendiculatus*" from the genital region of *Tubifex tubifex* and Mrázek's (1901) specimen from the same genus, *Tubifex*. This latter larval form was described by him as the larval stage of *C. laticeps* (= *C. mutabilis*). It possessed the characteristic "Fäserzellenstränge" of *C. laticeps* as well as some other morphological features. Mrázek therefore claimed this was the larval form and stressed the common possession of the "Fäserzellenstränge." This point unfortunately loses much of its significance when one realizes that there are at least three other species possessing these same characteristic tissues. Leuckart in the meantime (1878) had described *Archigetes sieboldi* from the *Tubifex*. This is considered by Lühe (1910) as a synonym of *A. appendiculatus*. Nybelin (1922) shows that *A. sieboldi* is the proper cognomen and therefore records *A. appendiculatus* as the synonym and points out that the original "*C. appendiculatus*" of Ratzel (1868) was probably a larval stage of *C. laticeps* as noted by Leuckart (1869). In 1908 Mrázek described a new and valid member of the genus, *A. brachyurus*. This form was easily distinguished by a shorter caudal vesicle and other morphological differences. Wisniewski (1928) describes a new member of this group, *A. cryptobothrius*. Ward (1911) records the presence of a Cestodarian from a fish. According to this preliminary note the parasite possessed some of the characters of both *Caryophyllaeus* and *Archigetes*.

Thanks to the kindness of Professor Frank Smith the author came into the possession of several parasitized Tubificid worms. These clearly belonged to the genus *Archigetes* and will be described in detail when more material is available. The author resolved to test out the hypotheses on the life history of the Cestodaria. Altho the results are negative the experiments will be outlined in the hope that it will prove an aid to other workers. Besides the theory of infection outlined in the preceding paragraphs which has been supported by various European workers the author wondered if there might not be some other explanation. It seemed more logical to assume that the eggs of all species except *Archigetes* were eaten by some Entomostracan and that after a developmental period had elapsed these in turn were eaten by a fish. This suggested cycle is similar to that worked out for other tapeworms [cf Janicki and Rosen (1917), Rosen (1918, 1919), Meggitt (1924), Hunter (1928, 1929) and Essex (1928, 1928a)]. A study of the contribu-

tions on the food of the hosts of the Caryophyllaeidae in North America clearly shows a predominance of Entomostraca over Tubificidae [see Forbes and Richardson (1908), Pearse (1918, 1921) and the reports of Greeley and Sibley of the New York State Department of Conservation on the Genesee and Oswego watersheds (1927 and 1928)]. Again the parasites have been found in numbers in the intestines, sometimes as many as several hundred in a single host. This is not significant in itself, but when coupled with the fact that in a study of over 5,000 Tubificidae from various localities less than 1 percent showed infection with Cestodaria it clearly indicates that great numbers of these worms must be eaten if they are to acquire several hundred parasites (all of which were in the same stage of development). Surely then is it not peculiar that these worms have not been recorded as constituting a more significant part of the diet of the fish?

The author decided to test the latter part of this theory by securing evidence on the rate of dissolution of Tubificidae in the stomachs of various hosts. Three species of fish were used, *Carpiodes carpio*, *Ictiobus cyprinella* and *I. bubalus*, in all 14 fish. Representatives of both the genera *Limnodrilus* and *Tubifex* were used in the experiments. The stomachs of the fish were aseptically opened and a worm placed therein. The Tubificidae were soon killed; the time required ranging from 3 minutes and 15 seconds to 10 minutes and 30 seconds. Complete dissolution occurred from 27 minutes and 35 seconds to 6 hours 25 minutes and 15 seconds (Table IV). Many of the fish used for stomach examinations are not killed immediately. Thus it is readily conceivable how the acid of the fish stomach would soon kill the

TABLE IV  
RATE OF DISSOLUTION OF TUBIFICIDAE IN FISH STOMACHS

Fish	Tubificidae	Dead in			Dissolved in		
		Hr.	Min.	Sec.	Hr.	Min.	Sec.
<i>Carpiodes carpio</i>	<i>Limnodrilus</i> sp.	0	8	30	6	25	15
<i>C. carpio</i>	<i>Limnodrilus</i> sp.	0	3	15	6	20	10
<i>C. carpio</i>	<i>Limnodrilus</i> sp.	0	3	20	6	12	15
<i>C. carpio</i>	<i>Tubifex</i> sp.	0	4	10	6	10	25
<i>C. carpio</i>	<i>Tubifex</i> sp.	0	10	30	4	5	10
<i>C. carpio</i>	<i>Tubifex</i> sp.	0	6	15	0	35	39
<i>Ictiobus cyprinella</i>	<i>Limnodrilus</i> sp.	0	8	45	4	46	5
<i>I. cyprinella</i>	<i>Limnodrilus</i> sp.	0	6	13	2	12	10
<i>I. cyprinella</i>	<i>Tubifex</i> sp.	0	6	00	0	27	35
<i>I. cyprinella</i>	<i>Tubifex</i> sp.	0	4	20	1	23	10
<i>Ictiobus bubalus</i>	<i>Limnodrilus</i> sp.	0	6	15	4	1	00
<i>I. bubalus</i>	<i>Limnodrilus</i> sp.	0	3	15	0	39	10
<i>I. bubalus</i>	<i>Tubifex</i> sp.	0	3	25	3	25	25
<i>I. bubalus</i>	<i>Tubifex</i> sp.	0	5	30	4	45	15



worm. It is but a step further to visualize the rapid disappearance of these worms by the grinding action of the muscular walls of the stomach aided by the presence of a few grains of sand or foreign matter. This would explain how the Tubificidae have but seldom been reported as food. Such an explanation leaves out of consideration the fact that in some cases at least the minute setae of these worms would have been noted, even tho the examination were rather cursory.

The existence or non-existence of operculate eggs amongst the Caryophyllaeidae is also a point worth investigating. This is very difficult to determine unless fresh material is available. Cooper (1920) reported that *Glaridacris catostomi* possessed operculate eggs. This means that there is some sort of a free swimming larval stage and that the first intermediate host might be actively sought out by the parasite, or devoured as a choice morsel by the host.

Some of the other experiments which were tried but failed to bring results will be briefly noted. Tubificidae from the Illinois River were carried to the U. S. Biological Fisheries Station at Fairport, Iowa, where infection experiments were attempted. Artificial inoculation per anus and mouth were tried without success. Likewise fish were planted in back waters, or sloughs, which had lost their connection with the Mississippi River. Such fish had been yielding 100 percent infection with young stages. Tubificid worms were not present and routine examinations of other possible intermediate hosts were negative. A period of high water re-established connection with the river and invalidated any results. Successful infection would have been significant since the Tubificid worms were absent.

Wisniewski (1928) has worked out experimentally the life cycle of his new species, *A. cryptobothrius*. He finds that this form possesses only one host, *Limnodrilus hoffmeisteri*. He secured positive infection in six of seven attempts and notes that the early stages of development may be encountered in different parts of the host, there being no special region where they occur when immature. The complete paper of Wisniewski will undoubtedly give the details of this interesting piece of work.

#### AFFINITIES OF THE CARYOPHYLLAEIDAE

Wisniewski (1928) follows his description of *A. cryptobothrius* with a brief account of some experiments on the life cycle of this form. He experimentally infected *L. hoffmeisteri* and found that as in the case of *A. seiboldi* there is but the one host, a Tubificid worm. As he points out there is no theoretical nor experimental grounds to longer assume that Archigetes may be a paedogenetic larval form of Caryophyllaeus. It does not preclude, however, so far as the evidence goes, the possibility of a similar Archigetes-like larva passing an embryonic period in the body cavity of Tubificid worms. However, it does seem extremely unlikely that this will prove to be



the case. It appears more probable that such forms as noted by D'Udekem, Ratzel and Mrázek and called *Caryophyllaeus* larvae by Nybelin (1922) and others will prove to be immature members of the genus *Archigetes*.

The question of the phylogenetic relationships of this group has been briefly touched previously. Wisniewski (1928) feels that he has sufficient evidence upon which to base his conclusion that the genus *Archigetes* represents a neotaenic proceroid larva of a *Bothriocephalid* tapeworm. To me it appears that to date our knowledge of the ontogeny of the related genera both in the *Bothriocephalidae* as well as the remainder of the *Caryophyllaeidae* is insufficient to warrant such conclusions. As pointed out earlier in the discussion we must wait until we secure a more detailed knowledge of the life histories of the members of these two groups until we can accurately determine their phylogenetic relationships. We are amassing evidence at a rapid pace for already we have considerable morphological evidence of apparent identities in structure between the groups. Nybelin (1922) realized this and attention has previously been called to such interesting forms as *Capingens singularis*, a cross section of whose scolex might readily be mistaken for one of the *Bothriocephalids* (Fig. 11). Likewise there are remarkably accurate reproductions in nature of the acetabular type of sucker (Figs. 16, 17), while Wisniewski (1928) has pointed to certain *Bothriocephalid* characteristics of his new form, *A. cryptobothrius*. In addition he suggests that the development of this species represents a neotenic *Bothriocephalid* proceroid larva. Certain points come to my mind, as the possession of a caudal vesicle bearing six embryonic hooks, the equivalent perhaps of the cercomer noted on all *Bothriocephalid* proceroids studied up to the present time. But what evidence do we have that this, as well as as the other similarities noted above, is not a case of convergence? Light will perhaps be thrown on this point when Wisniewski's completed paper appears. Until that time criticism is unjustified.

Ward (1911) discusses a parasite belonging to the *Caryophyllaeidae* from the intestine of fishes from the Illinois River. These resembled both the genus *Caryophyllaeus* and *Archigetes*, the former in the type of host and absence of a caudal vesicle and the latter in organization. This led Ward to two alternative hypotheses. In the first he suggests that the European form might have an undiscovered adult stage in some vertebrate host. In such a case the caudal vesicle would be lost as in *Caryophyllaeus* and the form he found. This possibility has been destroyed by Leuckart's and more recently Wisniewski's experiments, particularly the latter's in which he completes the life cycle of *A. cryptobothrius* and finds that it is confined to a single invertebrate host. Ward's second hypothesis is that the form noted by him may represent a higher stage in development. In such a case the European form would be a degenerate type which has lost the intermediate stage. Support for this conjecture is found in Pintner's interpreta-

tion of *Amphilina* as well as Woodland's work on this Cestodarian. Pintner (1903) claims that the location of *Amphilina* in the body cavity is evidence for this interpretation. Or as Ward suggests, the form described by him may indicate an adaptation whereby the invertebrate parasite has acquired a vertebrate host. The writer feels, however, that altho the suggestions are interesting the life history of all of the Caryophyllaeidae except *Archigetes* will prove to be somewhat similar to that of the other cestodes and will include an Entomostracan. Evidence for this view lies in the food of the hosts of these parasites which is largely Entomostracan. One other possibility remains and that is that direct infection occurs in the remainder of the Caryophyllaeidae as in *Archigetes*. All of the hosts both here and abroad are found amongst the Siluridae, Catostomidae or Cyprinidae, and all of these feed on or near the bottom and so might secure infection accidentally.

As for the remainder of the Caryophyllaeidae and the family as a whole but few words need be added. Nybelin (1922) in his excellent monograph on the Pseudophyllidea discusses the situation thoroly. He creates a new family, the Cyathcephalidae, to hold the Caryophyllaeidae of Leuckart and the Cyathcephalinae of Lühe. This is characterized as follows:

"Pseudophyllideen mit anapolytischer und acraspeder Strobila. Geschlechtsöffnungen flächenständig, median, die desselben Genitalkomplexes stets auf derselben Fläche der Strobila; Mündung des Uterus zwischen denen des Cirrus und der Vagina, in innigster Beziehung zur letzteren. Germarium median gelegen, ausgesprochen zweiflügelig mit lobierten Flügeln; das Gewebe der Seitenflügel viel kompakter als das der Querbrücke. Oötyp von gut ausgebildeten "Schalendrüssen" umgeben. Uterus gewunden, ohne lokale Erweiterung und mit echter Öffnung. Uterinaldrüsen gut ausgebildet. Eier dickschalig, gedeckelt. Geschlechtsreif in Fischen (Ausnahme *Archigetes*)."

The Caryophyllaeidae might well remain as a subfamily as created by Nybelin except that the characters indicated by him deal with features which are in part of less than subfamily and in part of more than subfamily importance. Furthermore the situation has been immensely complicated during the past few years by the quantity of new forms which have been described and with characters as narrow as those noted for his subfamily (see page 14). Earlier it was pointed out that Woodland (1923, 1926) went to the opposite extreme and deleted many valid genera. Granting that classification is entirely pragmatic it is equally evident that a system is needed which expresses the relationships within the family as clearly as possible as well as the interrelationships of the group. As noted in previous publications (Hunter 1927, 1929) the subfamily Caryophyllaeinae of Nybelin was taken out of the Cyathcephalidae and placed as an independent family of the Pseudophyllidea. This was given the diagnostic characters noted on

page 28 and was in turn subdivided into three subfamilies, the first of these, the Caryophyllaeinae, being modified from Nybelin's characterization of it. The Cyathocephalidae, the second family of the Pseudophyllidea and a close kin of the first, would then be composed of but a single family which might well be characterized by the following:

CYATHOCEPHALIDAE NYBELIN 1922

(= Cyathocephalinae Lühe) Char. emend.

Family diagnosis: Pseudophyllideans with stumpy strobila bearing but few proglottids. Poorly developed scolex and organs of attachment at anterior end. Reproductive system opens medianly, being multiply arranged one to each proglottid. Testes in two lateral fields, the larger part outside the longitudinal nerve strand. Vas deferens without external seminal vesicle; ductus ejaculatorius with distinct wall. Ovary bilobed; uterus and vagina open into common utero-vaginal canal guarded by a sphincter muscle. Vagina forms distinct receptaculum seminis and sharply set off ductus seminalis. Vitellaria annularly arranged up to median part of the proglottid. Eggs very small. Adult in intestine of fishes.

Such an arrangement has the advantage of keeping the Cyathocephalidae and Caryophyllaeidae on an equal footing and yet not so intimately associated as they would be were they in the same family. This appears more satisfactory since in reality a deep gulf exists between the two groups as is evidenced by the differences in strobilization, the Caryophyllaeidae being entirely monozooic while the Cyathocephalidae are polyzooic. Furthermore there may be a significant difference in the life history of these two groups, certainly there is evidence of this possibility as far as Archigetes is concerned, and it may prove to be true with the other genera of the family. In addition there are several clearly defined morphological differences such as the sphincter about the mouth of the utero-vaginal canal, the multiplication of the reproductive organs, the position of the testes in relation to the inner longitudinal muscles and the nerve strands. Clearly then there appear ample grounds for the separation of these two groups, the Caryophyllaeinae and Cyathocephalinae and their elevation to the rank of separate and equal families, the Caryophyllaeidae and Cyathocephalidae respectively.

PATHOLOGICAL EFFECT OF CESTODARIAN INFECTION

The Cestodaria are for the most part harmless parasites which have but little effect upon their host. They are typically free in the intestines but a few appear to have some pathological significance. Linton (1893) was the first to record any pathogenicity, citing *C. terebrans* which he found in pits in the mucosa where several individuals were crowded into a single pit. Altho this pit received but passing attention one cannot help but realize



that a number of these might constitute a serious obstruction in the alimentary canal. Cooper (1920) described and figured similar mucosal pits. These he described as follows:

"... but many larvae—forty-one in the case of the third fish in the table—were attached to the bottoms of deep pits in the mucosa of the pyloric region of the stomach. These pits were not mere depressions of the wall of the stomach but actual cavities . . . bordered by a pronounced annular thickening of the mucous membrane and as much as 2 mm. in diameter. Larvae ranging in size from almost the smallest met with to those near the adult stage in development were tightly crowded into these pits and at the same time strongly contracted longitudinally."

According to the figure shown in connection with this description one gains the impression that there is considerable proliferation of tissue.

More recently Bovien (1926) has described a very interesting situation in a catfish, *Clarias batrachus*. Here the parasite, *Djombangia penetrans*, bores its way through the muscular layers of the intestine carrying with it tissue from the submucosa. As Bovien points out this may have a detrimental effect since a simple bursting of this capsule places the body cavity in communication with the digestive tract. It appears to me to be the most important of any reported to date.

During the course of my collections only one form has been found which shows similar tendencies. This is *Monobothrium ingens*. It was found that from 1 to 7 adults might be present in a single pit. The smallest pit encountered measured 5 by 8 by 6 mm. in depth. The largest was 11 by 13 by 8 mm. These extruded into the intestine more than into the body cavity and in one instance two nearly closed the intestine. In every case the scolex of the parasite was found embedded in this proliferating tissue. This phenomenon suggests the possibility that the cells of uncertain function described in the neck of this and other Cestodaria may be glandular in nature and so secrete some substance which aids the parasite in its boring into its host. These cells may pass their products into small ducts which in turn lead to the exterior in this part of the scolex, or neck. Further evidence for the support of this theory lies in the fact that in case penetration of the tissues is not accomplished, abnormal growth of tissue appears instead. This explanation is further substantiated by the presence of similar groups of cells in the neck of *C. terebrans*, *G. catostomi*, and also in *G. hexacotyle*. In the case of the latter no information concerning its pathogenicity is available.

These four parasites, *C. terebrans*, *G. catostomi*, *D. penetrans* and *M. ingens* are the only Caryophyllaeidae known to have a pathogenic effect upon their host. In every case the injury appears to be of a mechanical nature. In *C. terebrans* the parasite is poorly equipped for such work since the scolex is unarmed. In *G. catostomi* the scolex has three pairs of loculi while in *M. ingens* which causes a more severe injury, the scolex is armed with 6 weak loculi and a terminal introvert. That there is actually any correlation



TABLE V. DISTRIBUTION OF CARYOPHYLLAEIDAE ACCORDING TO CONTINENTS

Continent	Subfamily	Genus	Species
North America	Caryophyllaeinae	Caryophyllaeus	<i>C. terebrans</i>
	"	Glaridacris	<i>G. catostomi</i>
	"	"	<i>G. hexacotyle</i>
	"	"	<i>G. laruei</i>
	"	"	<i>G. confusus</i>
	"	Monobothrium	<i>M. ingens</i>
	"	Biacetabulum	<i>B. infrequens</i>
	"	"	<i>B. meridianum</i>
	"	"	<i>B. giganteum</i>
	"	Hypocaryophyllaeus	<i>H. paratarius</i>
	Capingentinae	Pseudolytocestus	<i>P. differtus</i>
Europe	"	Capingens	<i>C. singularis</i>
	"	Spartoides	<i>S. wardi</i>
	Caryophyllaeinae	Caryophyllaeus	<i>C. laticeps</i>
	"	"	<i>C. caspicus</i>
	"	"	<i>C. fimbriceps</i>
	"	Monobothrium	<i>M. wagneri</i>
	"	Caryophyllaeides	<i>C. fennica</i>
	"	"	<i>C. skrajabini</i>
	"	Archigetes	<i>A. sieboldi</i>
	"	"	<i>A. brachyurus</i>
	"	"	<i>A. cryptobothrius</i>
Africa	Lytocestinae	Lytocestus	<i>L. filiformis</i>
	"	"	<i>L. chalmersius</i> (?)
	"	Monobothroides	<i>M. cunningtoni</i>
	"	Lytocestoides	<i>L. tanganyikae</i>
	Wenyoninae	Wenyonia	<i>W. virilis</i>
	"	"	<i>W. acuminata</i>
Asia	"	"	<i>W. minuata</i>
	Caryophyllaeinae	Caryophyllaeus	<i>C. syrdarjensis</i>
	"	"	<i>C. armeniacus</i>
	"	"	<i>C. gotoi</i>
	Lytocestinae	Lytocestus	<i>L. adhaerens</i>
Java	Lytocestinae	Djombangia	<i>D. penetrans</i>
	Caryophyllaeinae	Caryophyllaeus	<i>C. javanicus</i>
	"	"	<i>C. oxycephalus</i>
	"	"	<i>C. serialis</i>
	"	"	<i>C. tenuicollis</i>
	"	"	<i>C. microcephalus</i>
Australia	"	"	<i>C. acutus</i>
	Lytocestinae	Balanotaenia	<i>B. bancrofti</i>

between the type of scolex and the mucosal pit is improbable but the situation is none the less interesting. It should be borne in mind that actual penetration of the intestine itself cannot be so difficult since young larvae of a number of parasites regularly reach the body cavity of their host in this manner. *Proteocephalus ambloplitis* larvae do this in the second intermediate host when armed only with an invaginated scolex without hooks (Hunter 1928) and other examples may be found. Bovien cites *D. penetrans* and Marochina (1925) tells of the pathogenic effects of five intestinal parasites.

#### DISTRIBUTION OF CARYOPHYLLAEIDAE

The accompanying table lists the subfamilies, genera and species of the Caryophyllaeidae which are found on each continent. An examination of Table V shows that there are thirteen species recorded from North America. These fall into eight genera and two subfamilies; Europe follows with nine species, four genera and one subfamily; Africa is next with seven species, four genera and two subfamilies, while Java has seven species, two genera and two subfamilies. It is probable that this will be reduced to one subfamily when the material is re-examined. If Java is included with Asia, as it was in prehistoric times, the total for Asia would be eleven species, three genera and two subfamilies. Asia follows with four species, two genera, and two subfamilies, and Australia trails with one species. No species of this group have been reported from South America, probably because but little parasitological work has been done on the proper hosts on these continents. Nor are there any records from Great Britain, the East or West Indies, Iceland or Greenland.

The records are too meager to justify any broad conclusions as to the distribution of these Cestodaria over the larger land areas. One might expect to find the same species on different continents. This was found in the case of *Proteocephalus macrocephalus* (La Rue 1914). It is significant that genera have been reported from more than one continent. The genus *Caryophyllaeus* occurs in Europe, Asia, and North America. *Monobothrium* is likewise reported from Europe and North America while *Lytocestus* is present in Asia and Africa. Indeed it is probable that as investigations of fish parasites are carried on the distribution of the genera will be materially increased, and it is quite possible that identical species may be reported from the different continents.

#### FISH HARBORING TWO OR MORE SPECIES OF CARYOPHYLLAEIDAE

The accompanying table indicates that eight species of fish are known to harbor two or more species of the Caryophyllaeidae. These six species fall into three families, the Cyprinidae, Catostomidae and Siluridae (Table VI).

TABLE VI. FISH HARBORING MORE THAN ONE SPECIES OF CARYOPHYLLÆIDAE

Host	Species of Caryophyllæidae Harbored	Distribution of Parasite
<i>Abramis brama</i>	<i>Caryophyllæus laticeps</i> <i>Caryophyllæus skrjabini</i> <i>Caryophyllæus caspicus</i>	Sweden; Don River, Russia Don River, Russia Near Caspian Sea, Russia
<i>Cyprinus carpio</i>	<i>Caryophyllæus laticeps</i> <i>Caryophyllæus fimbriceps</i>	Europe and Africa Near Caspian Sea, Russia
<i>Catostomus commersonii</i>	<i>Glaridacris catostomi</i>  <i>Glaridacris laruei</i>	Douglas Lake, Mich. Burnt- side Lake, Minn.; Lake Erie, N. Y. Green Lake, Wisc.; Lake Mendota, Wisc.; Douglas Lake, Mich.
<i>Carpiodes carpio</i>	<i>Hypocaryophyllæus paratari</i>  <i>Capingens singularis</i> <i>Spartoides wardi</i>	Rock River, Ill.  Rock River, Ill. Rock River, Ill.
<i>Ictiobus bubalus</i>	<i>Caryophyllæus terebrans</i> <i>Glaridacris confusus</i> <i>Pseudolytcestus differtus</i>	Tallahatchie River, Miss. Mississippi River, Ia. Tallahatchie River, Miss.
<i>Ictiobus cyprinella</i>	<i>Monobothrium ingens</i> <i>Hypocaryophyllæus paratari</i> <i>Spartoides wardi</i>	Mississippi River, Minn. Mississippi River, Ia. Mississippi River, Minn.; Rock River, Ill.
<i>Clarias batrachus</i>	<i>Lytocestus indicus</i> <i>Djombangia penetrans</i> <i>Caryophyllæus javanicus</i> <i>Caryophyllæus oxycephalus</i> <i>Caryophyllæus serialis</i> <i>Caryophyllæus tenuicollis</i> <i>Caryophyllæus microcephalus</i> <i>Caryophyllæus acutus</i>	Nagpur, India Djombang, Java Djombang, Java. Djombang, Java Djombang, Java Djombang, Java Djombang, Java Djombang, Java
<i>Macrones nigriceps</i>	<i>Caryophyllæus microcephalus</i> <i>Caryophyllæus acutus</i>	Djombang, Java Djombang, Java

It is interesting to note that one of the species is the German carp, *Cyprinus carpio*. This fish was introduced into this country in 1877 according to Forbes and Richardson (1908).\* Essex and Hunter (1926) report that

\* De Kay places the date of the introduction of the German carp, *Cyprinus carpio*, into New York State, at 1831 (Smallwood and Smallwood, 1929). The Smallwoods furnish additional data on the scarcity of parasites in this fish.

"In Europe von Linstow and Lühe list sixteen helminths found in this fish: one nematode (larval stage), two Acanthocephala, eleven trematodes and two Cestodaria." Since then another Cestodarian parasite, *C. fimbriceps*, has been found in this same fish. Essex and Hunter (1926) examined 26 *Cyprinus carpio* but only found five parasitized, one with nematodes and four with Acanthocephala. None of the 26 harbored Cestodaria. Since the collection of those data this author examined thirteen more *C. carpio* and never found a Cestodarian parasite. The situation is interesting to say the least. Presumably the feeding habits of the European and American *Cyprinus carpio* are essentially the same. The dearth of Cestodarian and other parasites must lie then in the inability of the European forms to become established over here. This is more readily understood when one goes into the history of the introduction of these carp into this country (Essex and Hunter 1926: 154). The adult *C. carpio* were brought to Washington, D. C. in 1877 and bred in fish ponds. The young fish were then distributed to twenty-five states. It is evident that the life cycles of the parasites must have been broken and that the only parasites which the introduced carp has now are those which it has picked up in its new environment.

An analysis of these eight cases of multiple infection shows that in *Abramis brama* and *Cyprinus carpio* the different species occur on the same continent, but in widely separated localities, while in the other hosts there is some overlapping of regions. Thus *Ictiobus bubalus* taken from the same stream (Tallahatchie) harbors two different genera of parasites and a third from the same host from another connected river (the Mississippi) some distance away. Again *I. cyprinella* yields two distinct genera from the same locality and further down the river (Mississippi) it harbors a third. Still more striking is the case of *Carpiodes carpio* which sheltered three distinct genera and species from the same river (Rock). Upon the other hand *Catostomus commersonii* harbored two species from five widely scattered lakes, one of the lakes (Douglas Lake, Michigan) yielding both species. One of the most interesting hosts is the Silurid *Clarius batrachus* which harbors eight species and three genera from Asia and Java. To be sure, the generic number will undoubtedly be reduced upon further study since even the incomplete description given by Bovien (1926) shows characters which resemble those of the genus *Lytocestus*. Two genera come from Java and one from India. One other host from Java, *Macrones nigriceps* harbored two species from the same genus which also occurred in *Clarias batrachus*.



CARYOPHYLLAEIDAE OCCURRING IN TWO OR MORE  
SPECIES OF FISH

Eleven species of Caryophyllaeidae have been found to occur in more than one species of fish. These species are listed and are indicated by an asterisk (\*) in appended Table VII which gives a summary of the parasites and the distribution for all species. These species are *Caryophyllaeus laticeps*, *C. caspicus*, *C. terebrans*, *Glaridacris confusus*, *Caryophyllaeides fennica*, *Hypocaryophyllaeus paratarius*, *Biacetabulum giganteum*, *Capingens singularis*, *Spartoides wardi*, *Caryophyllaeus microcephalus* and *C. acutus*. As many of the hosts as possible have been carefully examined in the hope that some evidence might be adduced to indicate the relations existing between the parasite and its host.

*Caryophyllaeus laticeps*

Nybelin (1922) reports finding specimens of this species in *Abramis brama* from the fish market in Upsala, Sweden, on September 6, 1917 and May 29, 1918. Pepoff (1924) reports 30% infection of this same species taken from the same host from the delta of the River Don in 1918. In the case of the hosts the former was undoubtedly caught somewhere in Sweden, possibly from some of the lakes and streams near Upsala, while the latter was taken from the waters flowing into the Black Sea by way of the Sea of Azov, two localities widely separated. This suggests a wide distribution of this form and that an examination of the host from other locations may lead to additional geographical records. The general distribution of the German carp, *Cyprinus carpio* throughout Europe explains to some extent the wide distribution of this parasite as evidenced by the records of this host. Lühe (1910) lists 22 species of fish which harbor this parasite. Undoubtedly there has been some confusion and further study may reveal new species. Baylis (1928) adds another host, *Barbas tropidolepis*, from Lake Tanganyika, Africa.

*Caryophyllaeus caspicus*

According to the account of Miss Klopina this worm was present in two genera and three species of fish, *Abramis brama*, *A. sofa*, and *Vimba vimbra*. These hosts were examined by members of the Caspian Expedition of 1914–1915. No definite records as to the location of the hosts were available in the original article other than has been indicated above. However, it is probable that collections were made at the mouths of the major rivers (as the Volga, Ural, Emba, Kuma and Terek Rivers) emptying into the Caspian Sea.

*Caryophyllaeus terebrans*

Heart Lake in the southeastern corner of Yellowstone National Park in Wyoming is the type locality for this parasite. Since 1893 there have been

TABLE VII. DISTRIBUTION OF THE CARYOPHYLLAEIDAE ACCORDING TO HOSTS

Parasite	Host	Locality
* <i>Caryophyllaeus laticeps</i> (Pallas 1781)	<i>Abramis brama</i> <i>Cyprinus carpio</i> <i>Barbus tropidolepis</i> and 20 others noted by Lühe 1910	Sweden; Don R., Russia Europe L. Tanganyika, Africa
* <i>Caryophyllaeus terebrans</i> (Linton 1893)	<i>Catostomus ardens</i> <i>Ictiobus bubalus</i>	Heart Lake, Wyo. Tallahatchie R., Miss.
<i>Caryophyllaeus syrdarjensis</i> Skrjabin 1913	<i>Schizothorax intermedius</i>	Russo-Turkestan, Asia
<i>Caryophyllaeus armeniacus</i> Cholodkowsky 1915	<i>Capoëta</i> sp.	Armenian Russia, Asia
* <i>Caryophyllaeus caspicus</i> Klopina 1919	<i>Abramis brama</i> <i>A. sofa</i> <i>Vimba vimbra</i>	Near Caspian Sea, Russia Near Caspian Sea, Russia Near Caspian Sea, Russia
<i>Caryophyllaeus fimbriceps</i> Klopina 1919	<i>Cyprinus carpio</i>	Near Caspian Sea, Russia
<i>Caryophyllaeus javanicus</i> Bovien 1926	<i>Clarias batrachus</i>	Djombang, Java
<i>Caryophyllaeus oxycephalus</i> Bovien 1926	<i>Clarias batrachus</i>	Djombang, Java
<i>Caryophyllaeus serialis</i> Bovien 1926	<i>Clarias batrachus</i>	Djombang, Java
<i>Caryophyllaeus tenuicollis</i> Bovien 1926	<i>Clarias batrachus</i>	Djombang, Java
* <i>Caryophyllaeus microcephalus</i> Bovien 1926	<i>Clarias batrachus</i> <i>Macrones nigriceps</i>	Djombang, Java Djombang, Java
* <i>Caryophyllaeus acutus</i> Bovien 1926	<i>Clarias batrachus</i> <i>Macrones nigriceps</i>	Djombang, Java Djombang, Java
<i>Caryophyllaeus gotoi</i> Motomura 1927	<i>Misgurnus anguillicaudatus</i> (Cobitidae)	Kumkan R., Korea
<i>Monobothrium wageneri</i> (= <i>M. tuba</i> Diesing) Nybelin 1922	<i>Tinca chrysitis</i>	Italy

\* Indicates species considered under "Caryophyllaeidae occurring in two or more species of fish."

DISTRIBUTION OF THE CARYOPHYLLAEIDAE ACCORDING TO HOSTS (*continued*)

Parasite	Host	Locality
<i>Monobothrium ingens</i> Hunter 1927	<i>Ictiobus cyprinella</i>	Mississippi R., Minn.
<i>Glaridacris catostomi</i> Cooper 1920	<i>Catostomus commersonii</i>	Douglas L., Mich.; Burntside L., Minn.; Lake Erie, N. Y.
<i>Glaridacris hexacotyle</i> (Linton 1897)	<i>Catostomus</i> sp.	Gila and Salt Rivers, Ariz.
<i>Glaridacris laruei</i> (Lamont 1921)	<i>Catostomus commersonii</i>	Green Lake and L. Mendota, Wis.; Douglas L., Mich.
* <i>Glaridacris confusus</i> Hunter 1929	<i>Ictiobus</i> sp. <i>Dorosoma cepedianum</i> <i>Ictiobus bubalus</i>	Tallahatchie R., Miss. Tallahatchie R., Miss. Mississippi R., Ia.
* <i>Caryophyllaeides fennica</i> (Schneider 1902)	<i>Leuciscus</i> <i>erythrophthalmus</i> <i>L. idus</i> <i>L. rutilus</i>	Finnland Finnland Sweden
<i>Caryophyllaeides skrjabini</i> (Popoff 1924)	<i>Abramis brama</i>	Don R., Russia
<i>Biacetabulum infrequens</i> Hunter 1927	<i>Moxostoma anisurum</i>	Rock R., Ill.
<i>Biacetabulum meridianum</i> Hunter 1929	<i>Erimyzon sucetta</i>	Eno R., No. Carolina
* <i>Biacetabulum giganteum</i> Hunter 1929	<i>Ictiobus</i> sp. <i>I. bubalus</i>  <i>I. cyprinella</i>	Tallahatchie R., Miss. Tallahatchie R., Miss.; Mississippi R., Ia. Rock R., Ill.; Mississippi R., Minn.
* <i>Hypocaryophyllaeus paratarius</i> Hunter 1927	<i>Carpiodes carpio</i> <i>C. velifer</i> <i>I. cyprinella</i>	Rock R., Ill. Rock R., Ill. Mississippi R., Ia.
<i>Archigetes sieboldi</i> Leuckart 1878	Tubificidae	Europe
<i>Archigetes brachyurus</i> Mrázek 1908	Tubificidae	Europe
<i>Archigetes cryptobothrius</i> Wisniewski 1928	Tubificidae	Europe

DISTRIBUTION OF THE CARYOPHYLLAEIDAE ACCORDING TO HOSTS (*Concluded*)

Parasite	Host	Locality
<i>Lytocestus adhaerens</i> Cohn 1908	<i>Clarias fuscus</i>	Hongkong
<i>Lytocestus filiformis</i> (Woodland 1923)	<i>Mormyrus caschive</i>	Anglo-Egyptian Sudan
† <i>Lytocestus indicus</i> (Moghe 1925)	<i>Clarias batrachus</i>	India
<i>Balanotaenia bancrofti</i> Johnston 1924	<i>Tandanus tandanus</i>	Burnett R., Queens- land, Australia
<i>Monobothroides cunningtoni</i> Fuhrmann and Baer 1925	<i>Auchenoglanis occidentalis</i>	L. Tanganyika, Africa
<i>Monobothroides chalmersius</i> (?) (Wood- land 1924)	<i>Clarias anguillaris</i>	Anglo Egyptian Sudan
<i>Djombangia penetrans</i> Bovien 1926	<i>Clarias batrachus</i>	Djombang, Java
<i>Lytocestoides tanganyikae</i> Baylis 1928	<i>Alestes</i> sp. (?)	L. Tanganyika, Africa
* <i>Capingens singularis</i> Hunter 1927	<i>Carpiodes carpio</i> <i>Ictiobus urus</i>	Rock R., Ill. Mississippi R., Minn.
<i>Pseudolytocestus differtus</i> Hunter 1929	<i>Ictiobus bubalus</i>	Tallahatchie R., Miss.
* <i>Spartoides wardi</i> Hunter 1929	<i>I. cyprinella</i>	Rock R., Ill.; Mississippi R., Minn.
	<i>Carpiodes thompsoni</i>	Mississippi R., Minn.
	<i>C. carpio</i>	Mississippi R., Ia.
<i>Wenyonia virilis</i> Woodland 1923	<i>Synodontis schall</i>	Anglo-Egyptian Sudan
<i>Wenyonia acuminata</i> Woodland 1923	<i>S. membranaceus</i>	Anglo-Egyptian Sudan
<i>Wenyonia minuta</i> Woodland 1923	<i>Chrysichthys auratus</i>	Anglo-Egyptian Sudan

no other records of this form until Dr. Parke H. Simer made his collections in Mississippi in the spring of 1927. An examination of the parasites taken revealed the presence of *C. terebrans* in the intestine of *I. bubalus* taken from the Tallahatchie River. This river unites with the Yalobusha to form the Yazoo River which in turn empties into the Mississippi River above Vicksburg, Miss. The Mississippi River receives the Missouri as one of its major tributaries and this in turn is fed by the Yellowstone River which takes its origin from Yellowstone Lake in Yellowstone National Park; this lake is a relatively short distance from Heart Lake the type locality

† Woodland (1926) provisionally places this form in the genus *Lytocestus*. This was substantiated in a recent letter from Professor Moghe.



of this parasite. During the past glacial periods these lakes may have been connected and this would account for the appearance of this parasite in two such different watersheds, for Heart Lake is the head waters of the Snake River which flows into the Columbia River and thence to the Pacific.

The author spent several days on Heart Lake in the summer of 1925 trying to secure *Catostomus ardens*, but the attempt was unsuccessful.

#### *Glaridacris confusus*

This parasite was first found in *Ictiobus bubalus* taken from the Mississippi River near Fairport, Iowa. It was quite common in this host but was not found in *I. cyprinella* and *I. urus*, from the same locality. Dr. Parke H. Simer collected this parasite from *Ictiobus* sp. in the Tallahatchie River, Mississippi. The connection between this and the Mississippi River by the Yazoo River has been previously mentioned. It is probable since the waters are connected and since the other species of the genus *Ictiobus* did not harbor *G. confusus* that Dr. Simer's host was also *I. bubalus*.

One of the most interesting records is the finding of this parasite in *Dorosma cepedianum*. This fish is seldom parasitized and then only with *Acanthocephala* according to over four hundred examinations made (Van Cleave, 1916, Essex and Hunter, 1926). Furthermore this is the first record of a Cestodarian parasite in the Dorosomidae, which is in the order Isospondyli while the Catostomidae and Cyprinidae are in the Evertognathi. Since Dr. Simer examined a number of these fish and found but this one case of infection and since Essex and Hunter (1926) do not report any Cestodarian infection it appears that this was probably a case of accidental parasitism. This view is further substantiated by the existence of flood water during the time the collections were being made. Such a flood as the Mississippi River drainage experienced in 1927 would be very apt to upset the balance of fish food, and so would account for the presence of such a parasite as *G. confusus* (Hunter, 1929a).

#### *Caryophyllaeides fennica*

This parasite was reported from three different hosts from Finland and Sweden, *Leuciscus erythrophthalmus*, *L. idus*, and *L. rutilus*.

#### *Hypocaryophyllaeus paratarius*

This parasite was very common in the fish taken from the Rock and Mississippi rivers. Both *Carpionodes carpio* and *C. velifer* harbored *H. paratarius* when taken from the Rock River although similar hosts examined from the latter river near Fairport, Iowa did not yield this form; however the parasite was found in *Ictiobus cyprinella*. Since the feeding habits and the food of *Carpionodes* and *Ictiobus* are rather similar one might suppose that the host was largely a matter of chance among these and related forms.

*Capingens singularis*

*Capingens singularis* was found but twice in an examination of over 600 fish. It was recovered once from the stomach of *Carpiodes carpio* and once from *Ictiobus urus*. The former was taken from the Rock River and the latter from Lake Pepin, an expansion of the Mississippi River, between Minnesota and Wisconsin. Each infection occurred singly, and these were the only two records of this form ever found.

*Spartioides wardi*

*Spartioides wardi* was commonly found in *Ictiobus cyprinella* taken from both the Rock and Mississippi Rivers. The former empties into the Mississippi near Moline, Illinois which is less than twenty miles above the spot where the species was taken from the latter locality. Likewise *Carpiodes carpio* taken from the aforementioned localities yielded the same parasites. Another species of the same genus, *C. thompsoni*, which is limited in distribution to Lake Pepin in the Mississippi drainage was also found to shelter *S. wardi*. These four hosts and the three different localities indicate a very wide distribution for this parasite.

*Biacetabulum giganteum*

This species was reported from two hosts from the Tallahatchie River in Mississippi, *Ictiobus* sp. and *I. bubalus*. This latter host also harbored the same parasite when taken from the Mississippi River at Fairport, Iowa. There is nothing unusual about this since the host is found in numbers in both localities and is one of the most common buffalo fish. Still another host, *I. cyprinella*, when examined from the Rock River in Illinois and Lake Pepin in the upper Mississippi River between Wisconsin and Minnesota yielded *B. giganteum*. This host is likewise common in both of these regions. The records show wide distribution for this form.

*Caryophyllaeus microcephalus*

This parasite was recovered from two species of catfish, *Clarias batrachus* and *Macrones nigriceps*, from streams near Djombang, Java. From the records it appears that both hosts occurred in the same stream and the same general locality. The former acted as a host for five other species in Java and one from Asia. It is a well established geological fact that the entire archipelago off the tip of the Malay Peninsula was connected during the past geologic ages. This may help account for the distribution of these parasites on the comparatively isolated islands of that group. Incidentally it opens up some very interesting problems through a study of the hosts and their parasites in an attempt to determine which islands were connected to the mainland and which were always separated.

*Caryophyllaeus acutus*

This parasite was likewise recovered from *Clarias batrachus* and *Macrones nigriceps* which were taken in the vicinity of Djombang, Java.

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## EXPLANATION OF PLATES

## ABBREVIATIONS

<i>a</i>	acetabular sucker	<i>olm</i>	outer longitudinal muscle
<i>b</i>	bothrium	<i>om</i>	ovarian commissure
<i>bm</i>	basement membrane	<i>ot</i>	oötype
<i>c</i>	circular muscles of cuticula	<i>p</i>	post-ovarian vitelline duct
<i>cs</i>	cirrus sac	<i>r</i>	receptaculum seminis
<i>d</i>	ductus ejaculatorius	<i>s</i>	seminal vesicle
<i>e</i>	excretory canals	<i>sh</i>	gland cell of oötype
<i>ea</i>	ascending excretory canal	<i>sp</i>	sphincter muscle
<i>ed</i>	descending excretory canal	<i>t</i>	testis
<i>eb</i>	excretory bladder	<i>td</i>	terminal disc
<i>f</i>	fertilization chamber	<i>tr</i>	transverse muscle
<i>g</i>	ganglionic mass	<i>u</i>	uterus
<i>ga</i>	genital atrium	<i>u<sup>1</sup></i>	primary descending limb of uterus
<i>gm</i>	gland cell of parenchyma	<i>u<sup>2</sup></i>	ascending limb of uterus
<i>i</i>	inner longitudinal muscle	<i>u<sup>3</sup></i>	descending limb of uterus
<i>ii</i>	terminal introvert	<i>uv</i>	utero-vaginal canal
<i>l</i>	loculus	<i>v</i>	vagina
<i>lc</i>	longitudinal cuticular muscle	<i>vd</i>	vas deferens
<i>o</i>	ovary	<i>vd</i>	vitelline duct
<i>ob</i>	oblique muscle	<i>x</i>	successive stages
<i>oc</i>	oöcapt	<i>y</i>	in formation of
<i>od</i>	oviduct	<i>z</i>	vitelline follicles

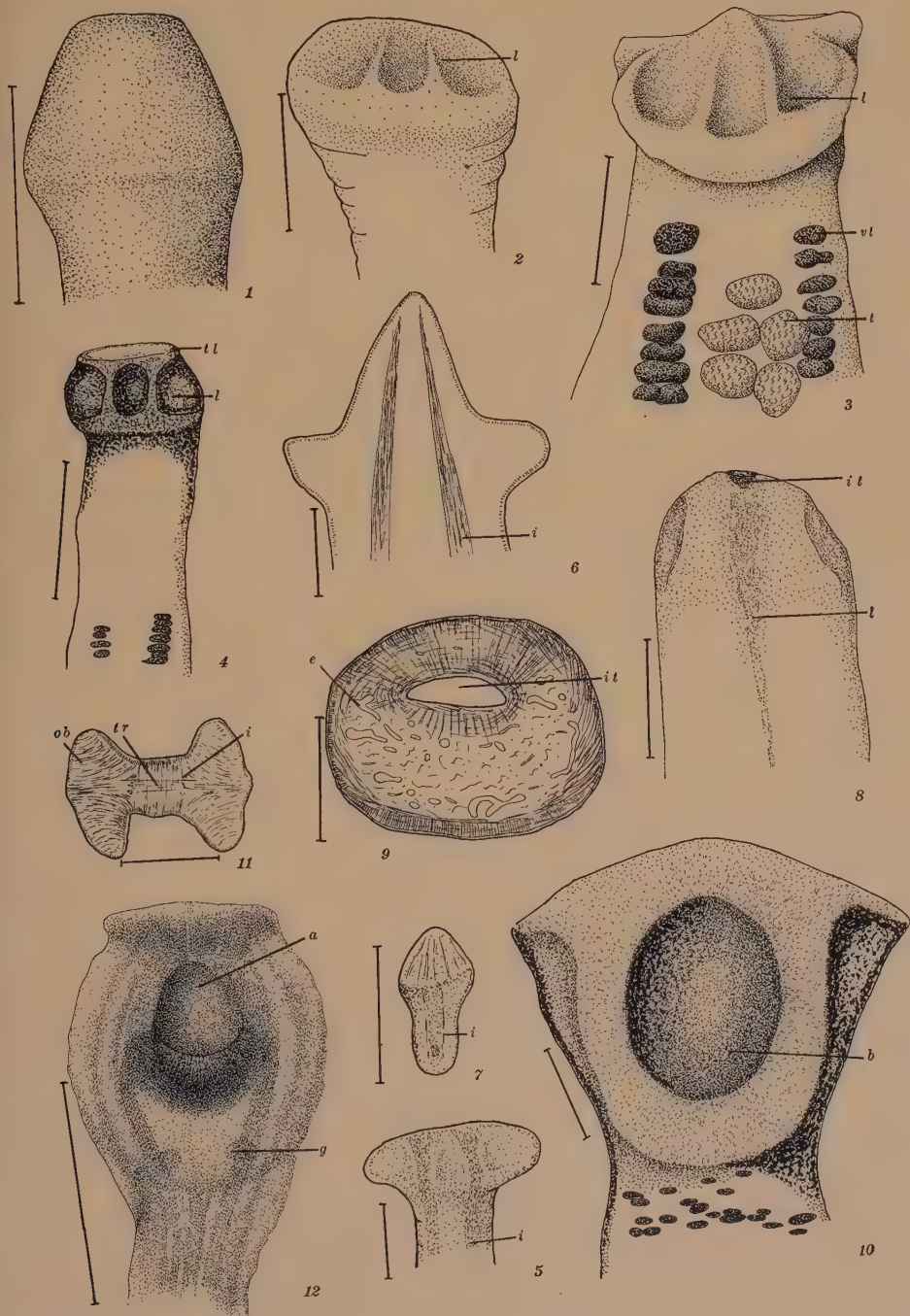
The lines in the figures have the following values: 0.02 mm. in figures 69, 77, 78, 81; 0.05 mm. in figures 76, 80, 84; 0.2 mm. in figures 5, 6, 27, 49, 54-60, 62-65, 68, 70, 85-90; and 0.5 mm. in all other figures.

## PLATE I

## EXPLANATION OF PLATE I

- FIG. 1. *Caryophyllaeus terebrans*, scolex.  
FIG. 2. *Glaridacris catostomi*, scolex.  
FIG. 3. *G. hexacotyle*, scolex.  
FIG. 4. *G. laruei*, scolex.  
FIG. 5. *Hypocaryophyllaeus paratarius*, scolex.  
FIG. 6. *H. paratarius*, sagittal section showing inner longitudinal muscles.  
FIG. 7. *H. paratarius*, larva.  
FIG. 8. *Monobothrium ingens*, scolex.  
FIG. 9. *M. ingens*, cross section through terminal introvert.  
FIG. 10. *Capingens singularis*, scolex.  
FIG. 11. *C. singularis*, cross section through bothria.  
FIG. 12. *Biacetabulum infrequens*, scolex.





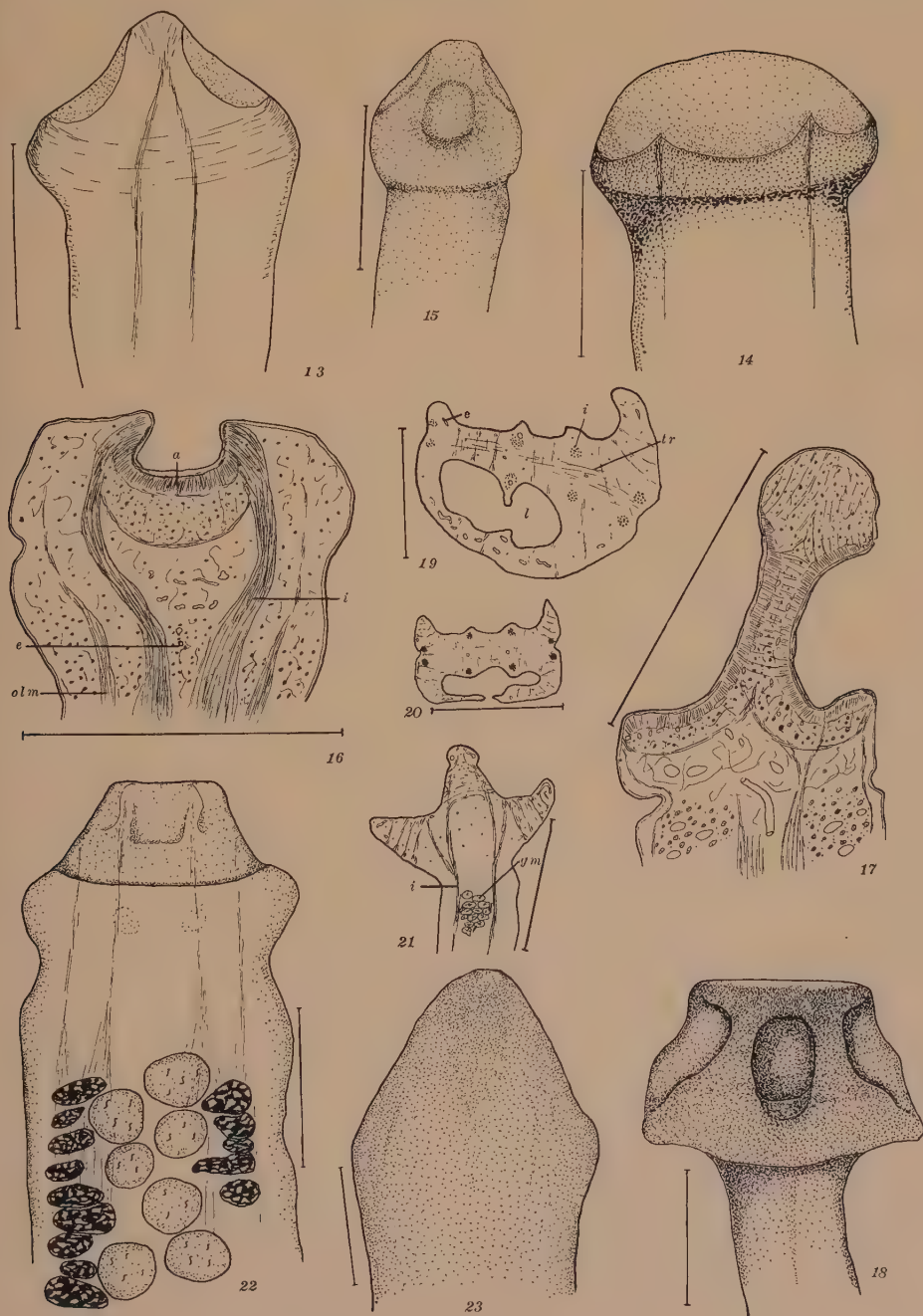


## PLATE II

## EXPLANATION OF PLATE II

- FIG. 13. *Spartoides wardi*, lateral view of scolex.  
FIG. 14. *S. wardi*, scolex.  
FIG. 15. *Biacetabulum meridianum*, scolex.  
FIG. 16. *B. infrequens*, frontal section, through acetabular sucker.  
FIG. 17. *B. infrequens*, sagittal section, through scolex.  
FIG. 18. *B. giganteum*, scolex.  
FIG. 19. *Glaridacris hexacotyle*, cross section, through scolex.  
FIG. 20. *G. hexacotyle*, cross section, through scolex.  
FIG. 21. *G. hexacotyle*, sagittal section, through scolex.  
FIG. 22. *G. confusus*, scolex.  
FIG. 23. *Pseudolytocestus differtus*, scolex.





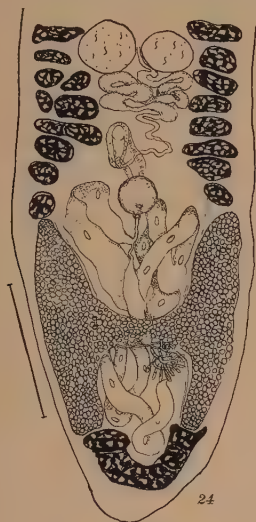


## PLATE III

## EXPLANATION OF PLATE III

- FIG. 24. *Glariidacris confusus*, toto, reproductive systems.  
FIG. 25. *G. catostomi*, toto, reproductive systems.  
FIG. 26. *Pseudolytocestus differtus*, toto, reproductive systems.  
FIG. 27. *Hypocaryophyllaeus paratarius*, cross section, through scolex.  
FIG. 28. *Spartoides wardi*, toto, reproductive systems.  
FIG. 29. *Monobothium ingens*, toto, reproductive systems.  
FIG. 30. *Caryophyllaeus terebrans*, toto, reproductive systems.  
FIG. 31. *C. terebrans*, frontal section, reproductive systems.

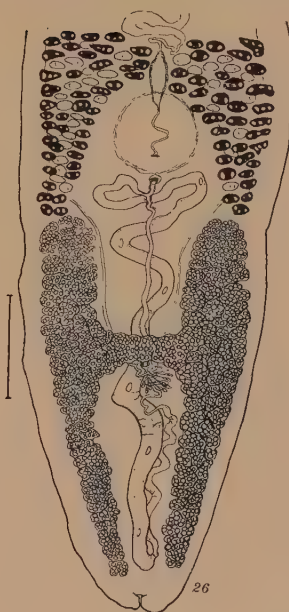




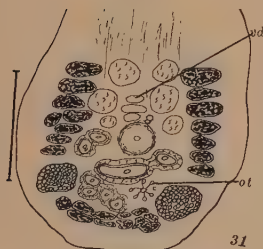
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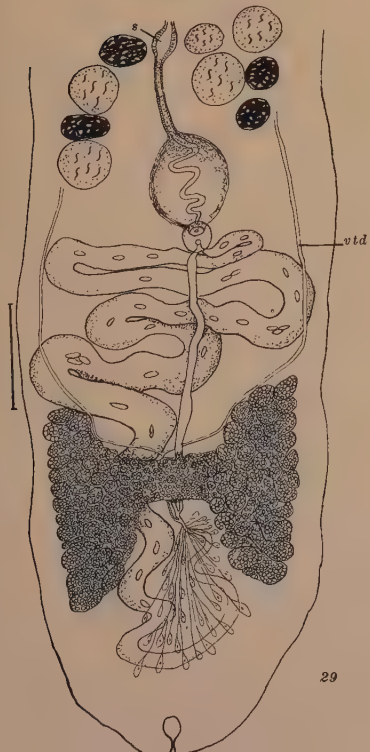
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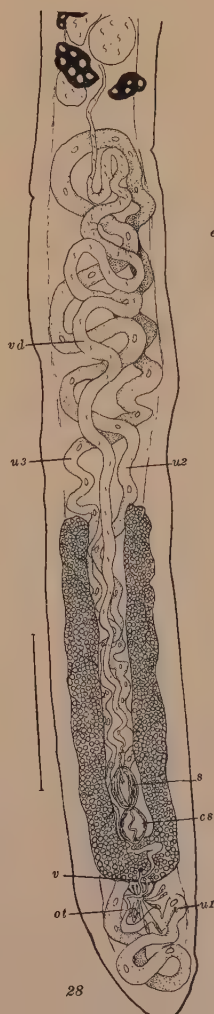
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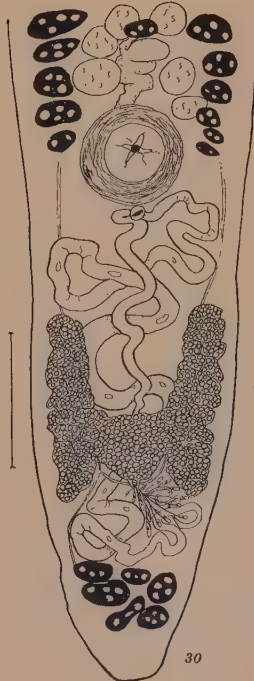
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## PLATE IV

## EXPLANATION OF PLATE IV

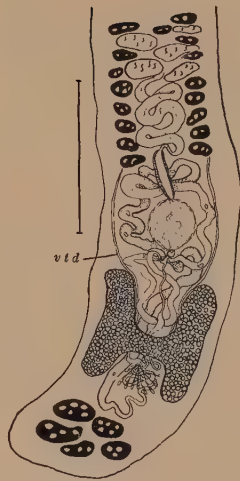
- FIG. 32. *Biacetabulum infrequens*, toto, reproductive systems.  
FIG. 33. *B. giganteum*, toto, reproductive systems.  
FIG. 34. *B. meridianum*, toto, reproductive systems.  
FIG. 35. *Capingens singularis*, toto, reproductive systems.  
FIG. 36. *Glaridacris laruei*, toto, reproductive systems.  
FIG. 37. *Hypocaryophyllaeus paratarius*, toto, reproductive systems.  
FIG. 38. *H. paratarius*, sagittal section, through reproductive systems.



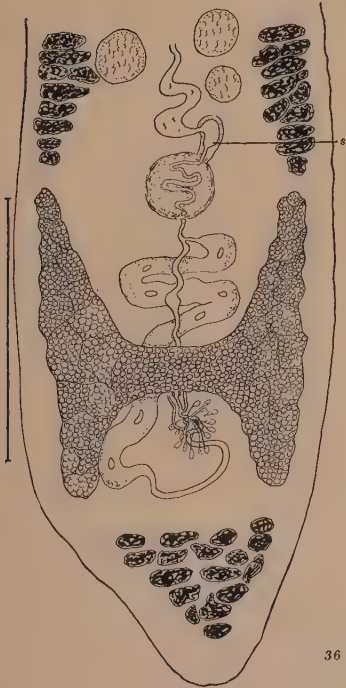
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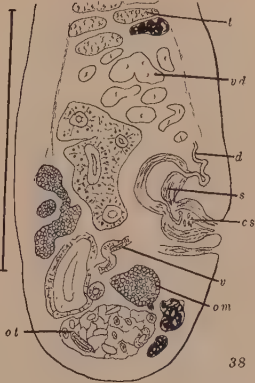
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## PLATE V

## EXPLANATION OF PLATE V

- FIG. 39. *Monobothrium ingens*, sagittal section, through reproductive systems.  
FIG. 40. *Biacetabulum giganteum*, sagittal section, through reproductive systems.  
FIG. 41. *Glaridacris hexacotyle*, sagittal section, through reproductive systems.  
FIG. 42. *G. hexacotyle*, cross section, through testes.  
FIG. 43. *G. confusus*, sagittal section, through reproductive systems.  
FIG. 44. *G. catostomi*, sagittal sections, through reproductive systems.  
FIG. 45. *G. catostomi*, cross section, through testes.  
FIG. 46. *Biacetabulum meridianum*, sagittal section, through reproductive systems.  
FIG. 47. *B. meridianum*, frontal section, through reproductive systems.  
FIG. 48. *B. infrequens*, sagittal section, through reproductive systems.  
FIG. 49. *Glaridacris laruei*, cross section, through testes.  
FIG. 50. *G. laruei*, sagittal section, through reproductive systems.  
FIG. 51. *Caryophyllaeus terebrans*, frontal section, through reproductive systems.  
FIG. 52. *Pseudolytocestus differtus*, sagittal section, through reproductive systems.

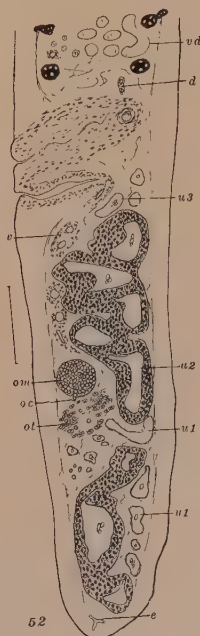
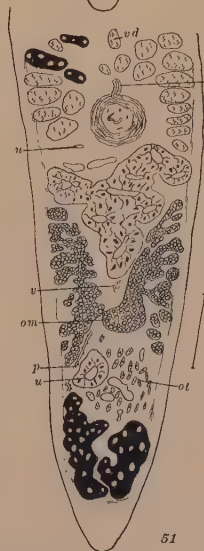
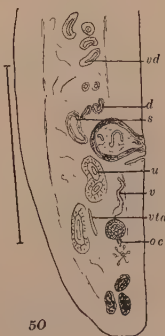
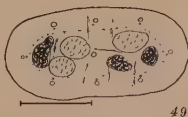
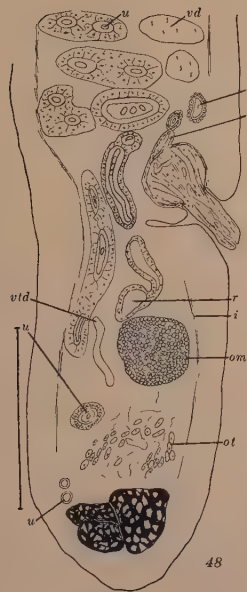
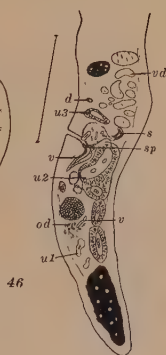
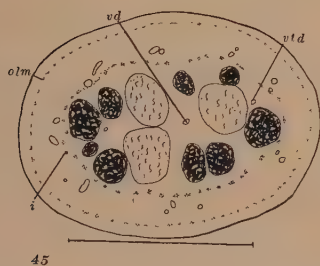
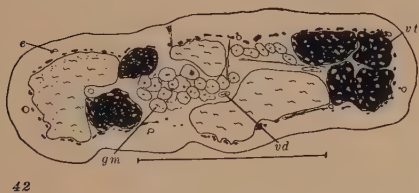
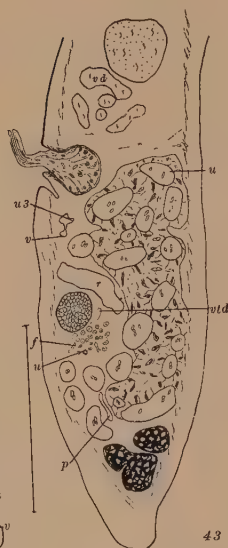
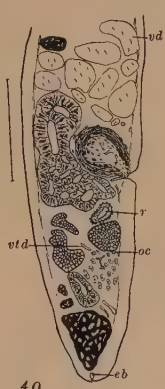
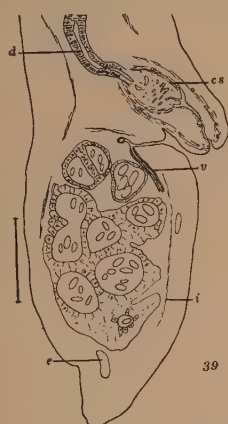


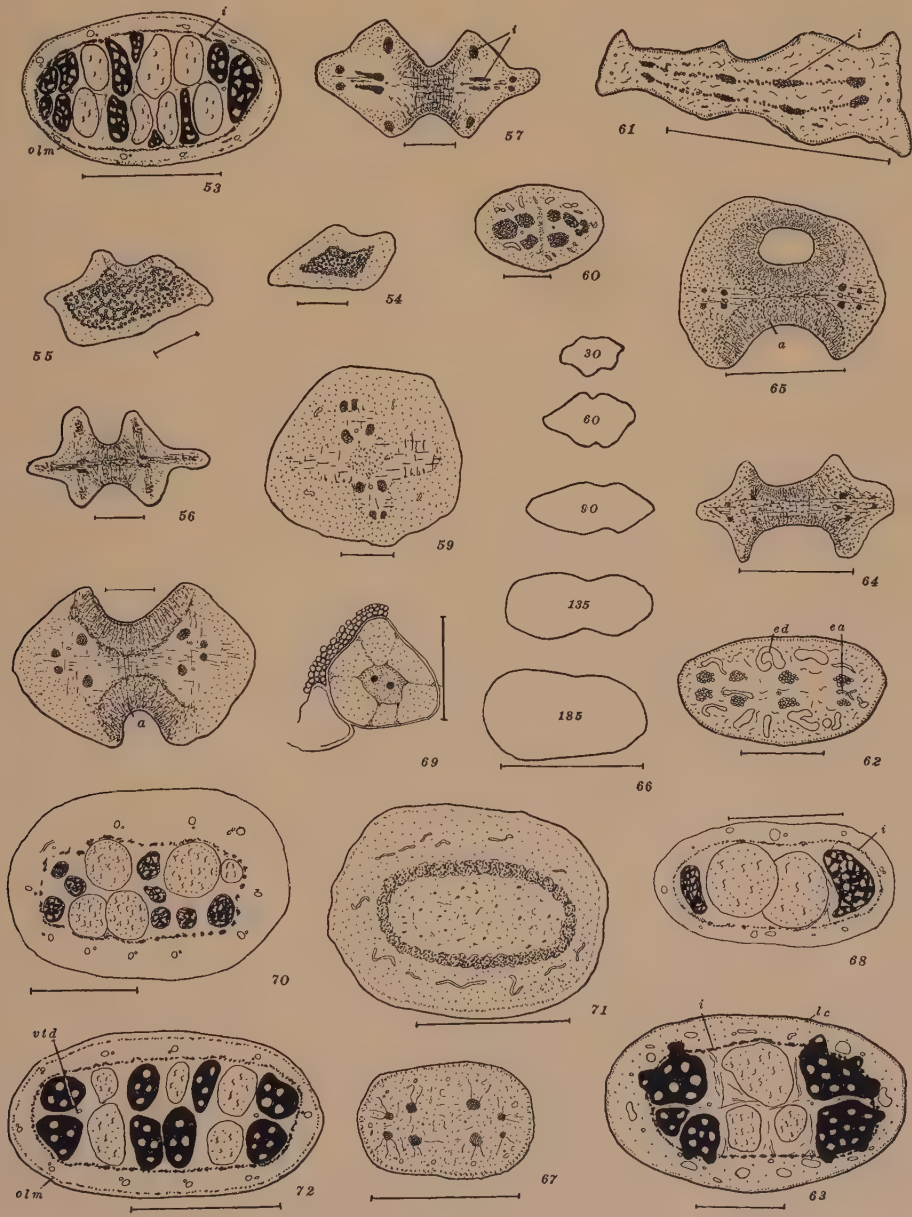




PLATE VI

## EXPLANATION OF PLATE VI

- FIG. 53. *Biacetabulum giganteum*, cross section, through testes.  
FIG. 54. *B. giganteum*, cross section, through scolex 40 $\mu$  from tip.  
FIG. 55. *B. giganteum*, cross section, through scolex 100 $\mu$  from tip.  
FIG. 56. *B. giganteum*, cross section, through scolex 200 $\mu$  from tip.  
FIG. 57. *B. giganteum*, cross section, through scolex 290 $\mu$  from tip.  
FIG. 58. *B. giganteum*, cross section, through scolex 490 $\mu$  from tip.  
FIG. 59. *B. giganteum*, cross section, through scolex 700 $\mu$  from tip.  
FIG. 60. *B. giganteum*, cross section, through scolex 1 mm. from tip.  
FIG. 61. *Spartoides wardi*, cross section, through scolex.  
FIG. 62. *S. wardi*, cross section, through base of scolex.  
FIG. 63. *S. wardi*, cross section, through testes.  
FIG. 64. *Biacetabulum meridianum*, cross section, through distal portion of scolex.  
FIG. 65. *B. meridianum*, cross section, through acetabular-like sucker.  
FIG. 66. *Glaridacris confusus*, outline of cross sections through scolex; figures indicate micra from distal extremity.  
FIG. 67. *G. confusus*, cross section, through base of scolex.  
FIG. 68. *G. confusus*, cross section, through testes.  
FIG. 69. *Biacetabulum infrequens*, cell from wall of seminal vesicle.  
FIG. 70. *B. infrequens*, cross section, through testes.  
FIG. 71. *Pseudolytocestus differtus*, cross section, through base of scolex.  
FIG. 72. *Caryophyllaeus terebrans*, cross section, through testes.





## PLATE VII



## EXPLANATION OF PLATE VII

- FIG. 73. *Capingens singularis*, cross section through testes.  
FIG. 74. *C. singularis*, cross section, through cirrus sac.  
FIG. 75. *C. singularis*, cross section, through utero-vaginal canal.  
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